ECOLOGICAL MONOGRAPHS

VOLUME 12 JANUARY, 1942 NUMBER 1

VEGETATION OF THE PRINCE WILLIAM SOUND REGION, ALASKA; WITH A BRIEF EXCURSION INTO POST-PLEISTOCENE CLIMATIC HISTORY

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VEGETATION OF THE PRINCE WILLIAM SOUND REGION, ALASKA; WITH A BRIEF EXCURSION INTO POST-PLEISTOCENE CLIMATIC HISTORY

INTRODUCTION

In 1916 I undertook a study of vegetational invasion following the recession of glaciers in the coastal region of southeastern Alaska. Glacier Bay was selected for first attention because it furnishes unparalleled opportunities for such study, due to phenomenal rapidity of recession and to a comparatively adequate knowledge of glacial behavior since the visit of the earliest European explorers nearly a century and a half ago. My first visit was followed by three others, in 1921, 1929 and 1935. The results, ecological and glaciological, have been presented in a number of papers (Cooper, 1923, 1931A, 1931B, 1931C, 1937, 1939A, 1939B). I was very glad when in 1935 the opportunity came to visit another portion of coastal Alaska where glacial behavior has been very different—where the glaciers today are as far advanced, or nearly as far, as they have been for at least several centuries. I wish to express once more my appreciation of the courtesy extended to me by Mr. William Osgood Field, Jr., in inviting me to participate in an expedition which covered both Glacier Bay and Prince William Sound.

The primary purpose of this paper is to describe the vegetation of the Prince William Sound region, with particular reference to its bearing upon recent glacial history. Quite naturally, comparison with Glacier Bay has yielded fruitful suggestions as to the vegetational and glacial history of coastal Alaska in general, and has even prompted an excursion still farther afield—into the rather controversial realm of post-Pleistocene climatic oscillations.

GEOGRAPHY, GLACIAL HISTORY, CLIMATE

Prince William Sound is a large, irregular body of water indenting the south coast of Alaska and lying just north of Lat. 60° and west of Long. 146° (Fig. 1). Its dimensions are roughly 70 miles east to west and 40 miles north to south. It is separated from the Gulf of Alaska by three large islands: Montague, Hinchinbrook and Hawkins. Another large one, Knight Island, and many smaller, lie within this barrier. The mainland north and west of the Sound is penetrated by numerous complex fiords, many of which contain one or more tidewater glaciers. Most of these are fed from the snowfields of the Chugach Mountains, the main coastal range in this region, whose highest peak (over 13,000 feet) is but 12 miles distant from the head of College Fiord. The glaciers of the southwestern fiords flow from the eastern of the two great mountain masses of the Kenai Peninsula. Our expedition visited all the fiords possessing

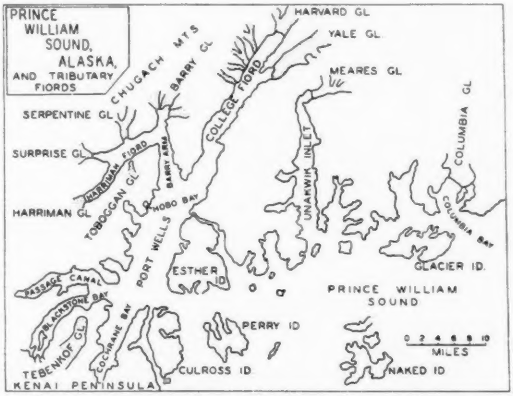


Fig. 1. Map of Prince William Sound showing principal features and localities studied.

tidal glaciers. Lack of time made it necessary for me to leave the party without seeing the two farthest southwestward—Port Nellie Juan and Icy Bay.

At the culmination of Wisconsin glaciation the whole of Prince William Sound was occupied by a great piedmont mass fed from the neighboring mountains (Tarr and Martin, 1914, Pl. CLXXXIV). Capps (1931) thinks it likely that a wide ice barrier bordered the coast of southern and southeastern Alaska, and that opposite Prince William Sound it "pushed out some 60 miles to sea." Tarr and Martin are less certain of this. Recession on a grand scale since Wisconsin time has brought about withdrawal of the ice from the sea except in the deep fiords.

As to the details of post-Wisconsin glacial history, almost up to the present, nothing is known with certainty. It must be assumed that recession was not continuous, and occasional submerged moraines described by Tarr and Martin doubtless mark the positions of temporary halts or readvances. In the final section of this paper a hypothetical sequence of events is suggested: a major period of ice contraction in middle post-Pleistocene time, followed by moderate expansion maintained, in the Prince William Sound region, up to the present.

Even the known recent history is rather sketchy. Vancouver (1801) visited several of the fiords in 1794. Davidson (1904) has collected the observations made here and elsewhere along the Alaska coast by various early Russian explorers. The first scientific survey of the region was made by the Harriman Alaska Expedition in 1899 (Muir, 1902; Gilbert, 1904). Grant and Higgins (1910-11, 1913) made studies in 1908 and 1909, and Tarr and Martin (1914) in 1909, 1910 and 1911. Field made his first investi-

gations in 1931 (Field, 1932); he continued them in our expedition of 1935 (Field, 1937). A few other visitors have made lesser contributions. These studies show varied behavior of glaciers during recent years. Some have advanced, some have receded, and there have been frequent reversals in trend; but nowhere is there evidence of recent major recession as at Glacier Bay. The most striking feature is the large number of glaciers which have been observed, during the last forty years, plowing into mature vegetation of great age. Details of history for the various fiords, so far as they are known, will be given in the body of the paper.

Climatic data for Prince William Sound are seanty. At only two stations have records been kept for a length of time sufficient to furnish reliable averages. Both of these—Cordova and Valdez—are situated at the eastern end of the Sound, and therefore not in the immediate vicinity of the localities studied. They are, however, fortunately placed. Cordova is close to the open sea, and therefore directly subject to oceanic influences. Valdez lies at the head of a fiord which penetrates the lofty Chugach Mountains. Although this inlet does not possess a major tide-water glacier, it is in most respects, even vegetationally, fairly comparable with such glacier-hemmed localities as College Fiord.

The pertinent data for these two stations are presented in Table 1. It is evident that the climate of the whole region is definitely oceanic. Temperatures in general are high for the latitude, and seasonal and diurnal ranges rather small. Precipitation is heavy, with a pronounced maximum in the autumn. A very small percentage takes the form of snow. In all, here is found a fair sample of the climate of the southern and southeastern coast of Alaska.

Cordova and Valdez portray conditions at sea level. For higher altitudes lower temperatures and greater precipitation must be assumed, with an increasing proportion of snow, doubtless attaining 100 percent among the highest peaks.

Between the two stations there are significant differences. Cordova has a mean annual temperature 5.3° higher than Valdez, and mean monthly temperatures higher in every case, with the differences much greater in winter. With regard to monthly maxima Cordova is higher in winter, Valdez in summer. The monthly minima at Cordova are consistently higher than at Valdez; the differences, again, are greater in winter. The contrast between the minima for the year—Cordova +6°, Valdez −10°—is particularly striking.

The most notable distinction is in total annual precipitation, Cordova receiving more than twice as much as Valdez. Seasonal distribution is about the same at the two stations. As to snowfall, if the data from 1937 are representative, Cordova receives a much smaller percentage of its precipitation in that form, but, on account of the greater total, the actual amount of snow is almost the same.

The climate of the inner ice-surrounded fiords is thus decidedly more severe than along the open coast; it is definitely less oceanic and more continental in character.

TABLE 1. Climatic data for Cordova and Valdez.

Mean annual and monthly temperatures, Fahrenheit

	Length of record (years)	Annual Mean	January	February	March	April	May	June	July	August	September	October	November	December
Cordova	25	41.0	27.1	30.1	32.3	37.6	44.6	51.0	54.9	54.5	49.0	42.0	39.1	29.0
Valdez	26	35.7	19.1	21.3	25.3	33.9	42.3	49.9	53.4	52.0	45.9	37.7	26.8	20.8

Monthly maximum temperatures, Fahrenheit, 1937

	January	February	March	April	May	June	July	August	September	October	November	December
Cordova	42	42	48	50	57	70	69	73	66	62	51	47
Valdez	37	37	44	52	63	76	71	75	70	60	40	43

Monthly minimum temperatures, Fahrenheit, 1937

	January	February	March	April	May	June	July	August	September	October	November	December
Cordova	18	6	18	29	31	39	44	40	39	31	27	8
Valdez	−1	−2	−2	20	26	37	38	37	30	28	12	−10

Mean annual and monthly precipitation, inches

	Length of record (years)	Annual Mean	January	February	March	April	May	June	July	August	September	October	November	December
Cordova	26	143.01	9.33	10.54	8.55	8.59	8.63	5.61	8.60	13.64	19.11	22.51	15.35	12.55
Valdez	24	60.25	4.54	4.92	4.34	2.95	2.74	2.06	3.56	6.29	8.85	8.29	6.00	5.71

Snowfall, inches, 1937

Cordova...... 95.3 = approx. 5 percent of total precipitation for year.
Valdez.......103.1 = " 17 " " " " " "

THE REGIONAL CLIMAX

COASTAL ALASKA IN GENERAL

The regional climax of the lower altitudes in the "panhandle" of southeastern Alaska, including the Alexander Archipelago and the adjacent mainland, is conifer forest in which three species are preponderant: western hemlock (*Tsuga heterophylla* (Raf.) Sargent), mountain hemlock (*T. mertensiana* (Bong.) Sargent), and Sitka spruce (*Picea sitchensis* (Bong.) Carr). Of these the first is by far the most abundant and generally distributed. Mountain hemlock is of special importance near the upper forest limit, but northward it comprises a considerable proportion of the forests even to sea level. Spruce is particularly characteristic of the lower altitudes but occurs throughout. The forests are practically unbroken except for avalanche tracks where the mountains rise

considerably above the timber and for very occasional spots of "tundra." The altitude of timberline ranges from 2,000 to 4,000 feet.

Northwest of Cross Sound, which marks the northern end of the archipelago, a narrow strip of the same type of forest follows the coast to the Copper River, a distance of 350 miles. In many places the forest is a mere fringe; it is even completely broken here and there where great glaciers reach the sea.

Beyond the Copper River the forests are again extensive. They cover the shores of Prince William Sound and the lower altitudes of the Kenai Peninsula. Their northwestern limit crosses Kodiak Island and the base of the Alaska Peninsula.

FORESTS

The regional climax of the lower altitudes around Prince William Sound is essentially an extension of that of southeastern Alaska, but with certain modifications.[1] The three dominating species of the southeastern climax are all present but in different proportions. Western hemlock is abundant eastward but very scarce westward. It was noted as locally dominant on Glacier Island, opposite the mouth of Columbia Bay, and as occasional on Heather Island, directly in front of the Columbia Glacier. One specimen was seen at each of two localities near Port Wells: Hobo Bay and in front of the Tebenkof Glacier. Mountain hemlock was present at every one of the 18 forested localities visited. The phrase "almost pure mountain hemlock" recurs repeatedly in my field notes. It must be regarded definitely as the characteristic tree of the northern shores of Prince William Sound. Sitka spruce was found at practically every station, but usually as a very minor constituent. In a few places it was noted as making half or more of the forest. No reasons for this local preponderance were evident. One other conifer, Alaska Cedar (*Chamaecyparis nootkatensis* (Lamb.) Spach) is present in the Prince William Sound region. I observed it at its northwestern limit on Glacier Island, where it is locally abundant and thrifty. A resident fox farmer reported diameters up to three feet. Sudworth (1908) notes its presence also on the mainland adjacent to Glacier Island and at two localities in eastern Prince William Sound. Munns (1938) adds no further stations. These isolated occurrences present an interesting phytogeographic problem, but the species is of no importance ecologically. The trees of all species vary in size according to local environment, the average diameter of mature individuals being 1 to 2 feet, the height 40 to 50 feet. Occasionally a diameter of more than 3 feet was noted and a height of 100 feet. Almost invariably the very large trees were spruces. The altitude of timberline is much lower than in southeastern Alaska, ranging (outside the narrow fiords) up to 2,000 feet.

The subordinate vegetation differs from that of the southeast Alaska climax only in being somewhat poorer in species; all those recorded here are prominent there. Among the tall shrubs, *Vaccinium ovalifolium* Smith is everywhere present and usually the most abundant. *Menziesia ferruginea* Smith is next in importance. Others are *Sorbus sitchensis* Roem., *Fatsia horrida* (Sm.) B. and H., *Sambucus pubens* Michx., *Cladothamnus pyrolaeflorus* Bong. and *Rubus spectabilis* Pursh. The last two species frequent the more open places. The ground cover is dominated by mosses, among which *Hylocomium proliferum* (L.) Lindb., *Rhitidiadelphus loreus* (L.) Warnst. and *Sphagnum* spp. are important. From a list of about 30 higher plants the following appear to be most frequent: *Blechnum spicant* (L.) With., *Dryopteris linnaeana* C. Chr., *D. oreopteris* (Ehrh.) Maxon, *D. dilatata* (Hoffm.) Gray, *Lycopodium annotinum* L., *Streptopus amplexifolius* (L.) DC, *Listera cordata* (L.) R. Br., *Coptis asplenifolia* Salisb., *Rubus pedatus* J. E. Sm., *Cornus canadensis* L., *Trientalis europaea* L. In areas transitional between forest and either of the two phases of the tundra true forest undergrowth is largely replaced by tundra species, and the trees are in open stand.

FIG. 2. Forest and tundra. Lower Harriman Fiord.

TUNDRA

The most striking difference between the regional climaxes of Prince William Sound and of southeastern Alaska is the much more conspicuous presence in the former of treeless areas covered by a solid mat of vegetation varying in character from place to place. I venture to denominate this general type as "tundra," a term which has been applied to a large number of arctic-alpine vegetation types, with much confusion as a natural result. Griggs,

[1] The description here given applies strictly to the areas personally seen by the writer: the coast and immediately adjacent islands from the mouth of the Copper River westward to the vicinity of Port Wells. Heller's description (1910) of the vegetation of the outer islands of the Sound, Hawkins, Hinchinbrook, Montague, Knight, and a number of smaller ones, indicates that the relative importance of the tree species differs somewhat from that of the region the writer studied. He reports that spruce is "the most abundant, widespread and largest tree," which fits with the well-known preference of the species for ocean shores. Western hemlock shows remarkable uniformity in distribution and "is confined chiefly to the immediate vicinity of the coast." Mountain hemlock is "almost as numerous individually as the spruce. A mountain species primarily, it here reaches the coast and becomes of universal distribution on the hillsides from timber-line to sea-level." Heller's region, which overlaps mine at not a single point, indicates forest composition closely similar to that of southeastern Alaska. The preponderance of mountain hemlock along the northern shores of the Sound may well be due to more "boreal" conditions close to the lofty Chugach Range.

I believe, has pointed out the best procedure in the use of the term. Following Middendorf, he suggests (1934B, p. 159) that we "use tundra in a geographic sense, applying it to all of the country of the treeless arctic." Certainly the two phases here described correspond with two of the several rather vague and intimately intergrading types which constitute arctic vegetation. One of these may be briefly termed "Empetrum heath," the other "Carex bog."

Empetrum heath. This type covers glaciated surfaces where conditions are relatively dry. (The qualifying adjective is quite necessary, since the whole region is more than "relatively" wet.) It characterizes projecting points along the shore, rock knolls, and well-drained areas generally. Bedrock is frequently visible here and there. The mat is comparatively thin, the accumulation of vegetable matter being usually a foot or less in thickness. The living surface layer consists basically of a mat of stems and roots of two dwarf shrubs, inextricably intertwined. *Empetrum nigrum* L. is everywhere present and usually most abundant; *Harrimanella stelleriana* (Pall.) Coville is a close second. *Phyllodoce glanduliflora* (Hook.) Coville is frequent, but not important in mass. *Vaccinium caespitosum* Michx. and *V. uliginosum* L. are notable constituents. Among the herbaceous contingent *Lutkea pectinata* (Pursh) Kuntze is very abundant, and *Lycopodium selago* L., *L. alpinum* L. and *L. sitchense* Rupr. are characteristic though relatively infrequent. Many others occur. My complete list, compiled from twelve stations, includes 40 spermatophytes and pteridophytes, of which only those listed above may be regarded as strictly typical. The forest flora is represented by a large number of species, among which *Lycopodium annotinum, Rubus pedatus* and *Cornus canadensis* are most frequent. There are many areas transitional with forest, which may be either open mat with scattered low scrubby trees, mostly mountain hemlocks, or relatively dense stands of trees with typical heath ground-cover. Bog plants are likewise common, especially *Nephrophyllidium crista-galli.* Areas intermediate in character between heath and bog are almost as frequent as typical examples of either. Lichens and mosses are fairly common but not important as basic constituents of the mat. On dry knolls species of Cladonia are abundant enough to give a grayish tone in a distant view.

Carex bog. Again I am introducing a controversial term, and will not give space to an elaborate defense of my usage, except to remark that a person having experience with the sedge bogs of the Great Lakes region finds it difficult to accept Sphagnum as an indispensable agent in bog formation, and therefore a criterion of whether or not a bog is a bog.

The type occupies depressions in the glaciated rock surfaces and flat areas where drainage is feeble. It also occurs on certain gentle slopes, which merit special attention after the general features have been covered. The thickness of the peat layer varies greatly, but is usually more than that of the heath; the maximum observed was about 4 feet. The living cover is principally a dense turf of sedges, in which *Carex nigricans* Mey. and *C. limosa* L. dominate. Sphagnum is present in considerable abundance; nevertheless the substratum is essentially sedge peat. The following species were collected: *Sphagnum capillaceum* var. *tenellum* (Schimp.) Andr., *S. girgensohnii* Russ., *S. lindbergii* Schimp., *S. papillosum* Lindb., *S. recurvum* Beauv., *S. riparium* Angstr., *S. subsecundum* Nees, *S. tenellum* Pers. The number of plant species characteristic of the bog is greater than in the heath. The following list of herbs and dwarf shrubs includes those most frequently observed; there are a number of others that should probably be included.

Sphagnum spp.
Selaginella selaginoides (L.) Link
Agrostis aequivalvis Trin.
Carex limosa L.
Carex nigricans Mey.
Eriophorum angustifolium Roth.
Tofieldia intermedia Rydb.
Habenaria hyperborea (L.) R. Br.
Habenaria unalaschensis (Spreng.) Wats.
Drosera rotundifolia L.
Rubus chamaemorus L.
Andromeda polifolia L.
Vaccinium oxycoccus L.
Gentiana douglasiana Bong.
Nephrophyllidium crista-galli (Menz.) Gilg
Swertia perennis L.
Pedicularis palustris L.

The frequence of areas transitional between bog and heath has already been noted. It is not surprising, therefore, to find *Vaccinium caespitosum* and *V. uliginosum* common on the bog, and Empetrum occurring frequently. Harrimanella is absent in typical areas. There is little exchange of species between bog and forest. The only conspicuous cases are the occurrence of low, matted mountain hemlocks on the bog and the presence of Sphagnum on the forest floor where it is very wet.

The hemlocks which grow upon the bog are of special interest. They occur in clumps or singly, are always small, with much dead wood, and frequently shrub-like with dense masses of foliage. In spite of small size they are of great age. One specimen (Fig.

FIG. 3. Forest and Carex bog. Mounds of vegetation around tree bases and covering large stones. The small but aged hemlock in center is described in text. Heather Island, close to front of Columbia Glacier.

3), found close to the front of the Columbia Glacier on Heather Island, was 6 feet tall and 5 inches in diameter. It had a small contorted head with a few tufts of living foliage. A basal section was brought home and the rings were counted with a microscope; it was 420 years old. The bases of these small ancient trees are often covered with a dense growth of vegetation which produces a mound of considerable size (Fig. 3). Nearby mounds, identical in vegetational make-up but without trees, were found to contain as nuclei sometimes old stumps, sometimes small glacial boulders. The covering mat is often 6 inches thick and is densely filled with stems and roots. Empetrum makes the bulk of it; many species are found which are characteristic of the heath, and forest herbs and mosses are also present. These mounds are essentially miniature islands of Empetrum heath, standing above the level of saturation.

Small ponds are frequent upon the bogs, usually an acre or less in extent. They occur in undrained hollows of the underlying rock surfaces, and also in step-like series upon gentle open slopes (Fig. 4). The

FIG. 4. Pools in Carex bog. *Sparganium angustifolium* in water. Heather Island, Columbia Bay.

latter type presents an interesting problem. The pool fills to the brim a basin with walls of hard peat, which are vertical or even overhanging and as much as 4 feet in height. The water moves from pool to pool either by seepage or over the edge in a miniature cascade. Often the peat dams separating the ponds are very narrow and sinuous in outline. The whole reminds one strongly of a series of small, very ancient and overgrown beaver dams. I have seen a similar series of peat-dammed pools in steps near Long's Peak, Colorado, in the subalpine forest just below timberline (10,500 ft.).

The origin of pools upon open slopes, bounded and separated by parapets of peat, is not clear. A possible clue may be suggested: occasional mats of Carex (principally *C. limosa*) and associated species found in a few places growing among scattered debris resting upon rock surfaces. Starting here where a foothold is offered, this vegetation may thicken upward without spreading much over adjacent clean surfaces, which, if enclosed, become water-covered. As the peat masses increase in height, the pools increase in depth. Slight horizontal increase in the mat as it grows upward would account for the overhang of the sides. Intensive search ought to reveal various stages in development.

The pools support a rather sparse aquatic flora. The following species were noted: *Potamogeton diversifolius* Raf., *Sparganium angustifolium* Michx., *Nymphozanthus polysepalus* (Engelm.) Fernald, *Hippuris vulgaris* L., *Menyanthes trifoliata* L. The last two species were marginal in shallow pools. *Sphagnum subsecundum* Nees and *S. lindbergii* were also found submerged, growing in considerable abundance around the margins. In some cases this may have been due to an unusually high water level, since other plants growing with them, definitely not aquatics, were entirely covered by water.

Griggs (1936), in describing the vegetation of the Katmai district, just west of the present forest margin, gives "heath" as one of the most important types of tundra and considers it "the most characteristically arctic" of them all. This is like the heath of Prince William Sound in the predominance of Empetrum, but the list of accessory species is quite different. It is characterized by multitudinous hollows, often water-filled, separated by ridges built fundamentally of plant materials. Superficially these suggest the bog pools already described, but their regular form and arrangement set them somewhat apart. Griggs notes also the presence of bogs, in which the basis is Sphagnum; the species list he gives differs considerably from mine. Although there is not exact agreement, the heath-bog combination of the Katmai district may fairly be considered as ecologically equivalent to the corresponding pair of types at Prince William Sound.

INTER-RELATIONS OF BOG, HEATH, AND FOREST

In a vegetation complex such as the present, if one reasons in the orthodox way, the forest must be regarded as climax and heath and bog as successional stages; and there is definite field evidence supporting this view. The forest occupies the major part of the area and the better-drained sites—those which are neither very wet nor very dry (for the region). Unquestionably certain changes are in progress tending toward replacement of heath and bog by forest: extension and thickening of the heath mat and bog deposits, together with slow extinction of the pools, resulting in general improvement in aeration and thus more favorable conditions for establishment of trees. On the other hand, in certain bog localities, especially where Sphagnum is abundant, the building up of the peat seems to be accompanied by a rise of the water table, as in the "raised bogs" of northeast America. In such places actual recession of the forest may be the result. The dead peat-covered stumps upon the bog are suggestive in this connection. It is clear that the period of rapid successional change which followed immediately upon the disappearance of the ice is now long past; present changes are so slow as to be barely perceptible, and the general trend cannot

be determined with certainty. The most logical procedure seems to be to treat the entire complex as a transition between the unbroken forest climax to the southeast and the arctic tundra climax lying to the west.

THE INNER FIORDS

Vegetation in General

My studies covered six major fiords penetrating the mainland north and west of the Sound. Three of these, Columbia Bay, Unakwik Inlet and Passage Canal, have vegetation essentially like that bordering the outer waters. The only special features are the more or less frequent avalanche tracks and the preponderance of heath over bog, because, on account of the abruptness of the walls, suitable areas for bog development are uncommon. The others, College Fiord, Harriman Fiord and Blackstone Bay, are quite different. Forest is reduced to small patches, and alder thicket is the most conspicuous type. Possible correlation of vegetational with climatic differences will be considered in a later section.

The alder thicket (*Alnus sinuata* (Regel) Rydb.) fills the broader avalanche tracks in fiords of the first group and mantles vast slopes in those of the second. It varies greatly in continuity and density; where the slopes are very steep it occupies only the ledges. It attains its best development on alluvial fans along the shore, where the bushes may be 25 feet tall. Here also are very large specimens of *Salix alaxensis* (And.) Coville, rising well above the alders. The undergrowth in such places is abundant and varied. The small shrubs are *Ribes laxiflorum* Pursh., *Rubus spectabilis*, *Fatsia horrida*, *Vaccinium ovalifolium*, and *Sambucus pubens*. The list of herbs is similar to that of the forest. Upon open slopes the alders are much lower, and smaller bush willows are added: *Salix barclayi* Anders., *S. commutata* Bebb, *S. sitchensis* Bong.

Several other communities occur in the fiords of the second group. In the aggregate they occupy considerable space but they are so poorly defined that concise description is difficult. A thicket of low shrubs other than willow and alder occurs frequently, in which *Rubus spectabilis* usually dominates. A tall-herb community is characteristic of watercourse margins; here *Veratrum viride* Ait., *Heracleum lanatum* Michx. and *Senecio triangularis* Hook. are conspicuous. In similar places one sometimes encounters "thickets" of the tall lady-fern, *Athyrium filix-foemina* (L.) Roth., so dense as to be difficult of penetration. Open moist flats and slopes, probably where snow lies late, support a rich growth of herbs of lower stature, which provide the finest flower displays. Among the more frequent are the following:

Aconitum delphinifolium DC	*Sanguisorba sitchensis* Mey.
Aquilegia formosa Fish.	*Geranium erianthum* DC
Ranunculus eschscholtzii Schlecht.	*Epilobium angustifolium* L.
Epilobium latifolium L.	*Achillea borealis* Bong.
Epilobium luteum Hook.	*Arnica chamissonis* Less.
Polemonium acutiflorum Willd.	*Artemisia arctica* Less.
	Aster foliaceus Lindl.
Mimulus langsdorfii Donn	*Petasites frigida* (L.) Fries
Valeriana sitchensis Bong.	

Certain areas, particularly in Blackstone Bay, bear a dense meadow growth of waist-high *Calamagrostis scabra* Presl. Finally there are the rock crevices, mostly well watered, which give anchorage to various ferns (*Dryopteris dilatata* (Hoffm.) Gray, *D. oreopteris*, *Cryptogramma achrostichoides* R. Br., *Cystopteris fragilis* (L.) Bernh.), several saxifrages, and a miscellaneous assemblage derived from the other communities of the region.

Each fiord has its own special features, and since many of these are of importance in interpretation of the vegetational and glacial history, it is necessary to describe them individually. The group of forested fiords will be considered first.

Columbia Bay

Columbia Bay may not strictly be termed a fiord (Figs. 1, 7). It is a short, broad indentation 4 miles long and 3 wide at the entrance. Heather Island, 3 miles long, divides it into two parts, of which the western is larger and deeper. Columbia Glacier, with a convex, sinuous front 6½ miles in total length, bounds it on the north. The westernmost portion presents an imposing tidal cliff nearly 2½ miles long. The next half mile, projecting conspicuously, rests upon a group of islets connected at low tide with Heather Island. There follows the eastern tidal cliff, less impressive than the other, 2 miles long, rising from shallow water. The easternmost section is in contact with a complex of rocky knobs, glacial deposits, and marginal lakes and streams.

Recorded glacial history. As in Glacier Bay, so here, Vancouver (1801) provides a starting point. His description and map indicate that the glacier front in 1794 was not notably different from today. Applegate (see Davidson, 1904) found conditions approximately the same in 1887. The events of the intervening century are unknown. The first careful study was made by Gilbert (1904) as a member of the Harriman Alaska Expedition. He noted that a few years before his visit in 1899 the ice had reached a maximum, invading and destroying mature forest at the three points where it rests on land. Recession of a few hundred feet was followed by another advance, described by Grant and Higgins (1913), and in great detail by Tarr and Martin (1914). By 1910 the ice had recovered all lost ground and was again plowing into the forest. The advance continued till after 1914 (Field, 1932). Recession again occurred until 1931, when Field (1932) noted incipient symptoms of a third advance, which were confirmed during our visit of 1935. The ice margin had moved forward on all fronts, but still fell short of the earlier maximum except at one point on Heather

Island. The recent history has been summarized by Field as follows (1937, p. 70): "Since 1899 . . . the terminus of the Columbia Glacier has fluctuated back and forth between limits 1,000 feet apart on the west side and nearly three quarters of a mile on the east." It is quite possible that no changes more significant than those observed have occurred since Vancouver's visit, nearly a century and a half ago.

Vegetation. Since Columbia Bay is not a typical fiord, it is not surprising to find the vegetation very similar to the climax-complex described for the open shores of the Sound (Fig. 5). The mountain slopes

FIG. 5. Forest and tundra near west end of Columbia ice cliff.

bounding the bay are clothed to a height of about 1,500 feet with dense mature forest, in which mountain hemlock predominates. Because of the lowness of the mountains they are unscarred by avalanches. Heather Island, a rounded mass of glaciated rock, exhibits to perfection the various phases of the vegetation-complex; the surface is about evenly divided between forest, heath, and bog with many pools.

Along the island terminus of the glacier, I saw in 1935 the wreckage resulting from ice attack—smashed and overturned trees, and great crumpled rolls of thick bog peat (Fig. 6). Tarr and Martin in 1909 and 1910 observed the advance in active progress. For a vivid impression of what happens to vegetation under the irresistible onslaught of a forward-moving glacier the reader is referred to their account (1914, pp. 263-282). They state (p. 271) that upon the Heather Island front "the ice was surely farther out than it had been for fifty to one hundred years . . . [for] some of the trees were a foot in diameter and from fifty to one hundred years old." Whatever the basis for their estimate, this is an understatement. The small hemlock of Figure 3, previously described, grew here within 300 feet of the limit of recent ice advance. Its age—420 years plus—makes it safe to say that the ice has not been farther forward for at least 500 years.

FIG. 6. Forest wrecked by recent advance of Columbia Glacier. Pioneer vegetation in foreground has come in since 1914. Near A, Fig. 7.

The mountain-side forest does not cease at the ice front, but continues northward along the slopes above the glacier surface, becoming gradually more and more patchy. The non-forested areas are probably mainly heath. The lower edge is sharply defined, and is separated from the ice by a very narrow barren zone, developed since the recent maximum. From a high point Tarr and Martin (1914, p. 286) were able to distinguish forest west of the glacier for a distance of at least 6 miles from the terminus, and also upon a great nunatak which is equally far removed. They consider this good evidence of notable contraction of the ice at some period before Gilbert's maximum of the last decade of the nineteenth century. With this the writer thoroughly agrees.

The landscape here is an exact counterpart of Glacier Bay as it appeared during the most recent ice maximum, about two centuries ago (Cooper, 1923, 1937). Glacier Bay was then filled by a huge trunk glacier which during its expansion had overwhelmed the vegetation upon the lower slopes. A strip of forest and heath lying above the ice escaped destruction, and this is logically to be associated with remains of forest uncovered near sea level by recession of the glaciers as proof of an important glacial minimum preceding the late advance. It is easy to visualize a corresponding period of contracted ice at Columbia Bay, with extension of the bay 6 miles or more northward at the expense of the glacier, and with shores completely mantled with forest and heath. Advance is assumed to have destroyed the vegetation up to the sharply cut margin that can be seen today. It is of course conceivable, as Martin points out, that vegetation may have migrated along the slopes above the ice, and even reached the nunatak, with the glacier just maintaining itself at its present stand. But in the light of what is known of the behavior of Alaskan glaciers, and in particular remembering the demonstrated history of Glacier Bay, it seems far more reasonable to assume changes in the ice, even great ones, than a lengthy period of quiescence.

Invasion of areas left bare by recent recession. In 1914 the ice front was advancing into mature vegetation. Age counts of the oldest woody plants at various points in the barren zone indicate that advance was succeeded by recession very soon after that date. The plant population of the barren zone at the time

Photograph by W. O. Field, Jr.

FIG. 7. Aerial view of front of Columbia Glacier from the northeast. Heather Island at left of projecting ice. Line shows approximate limit of recent advance. A, B, C, localities where pioneer vegetation was studied.

of our visit had thus become established in less than 21 years. Listing of the plants growing in three typical localities (Fig. 7, A, B, C) yielded a total of 78 species. It was a very miscellaneous assemblage, with representatives from every community of the region. The species which one is accustomed to regard as normal pioneers—*Equisetum variegatum, Epilobium latifolium, Salix arctica* and *Rhacomitrium canescens*—were present, but not at all dominating. The usual shrub stage was represented by alder and several willows, the forest by spruce, occasional mountain hemlocks, and a few forest herbs. Bog and heath plants were frequent, also species characteristic of rock crevices, and a number difficult to assign to any definite community. Even the morainic pools contained the beginnings of their characteristic flora: *Potamogeton pusillus* L., *Sparganium angustifolium* Michx., *Philonotis fontana* Brid., and around the edges *Eleocharis palustris* (L.) R. and S., *Eriophorum chamissonis* C. A. Mey., *Carex aquatilis* Wahlenb., *C. rostrata* Stokes, *C. spectabilis* Dewey, *Juncus balticus* (Willd.), *J. castaneus* Smith. The plant cover at A, Figure 7 (see also Fig. 8) was dense, with little bare ground showing; at B and C it was less so.

It seems that when bare soil is exposed contiguous to varied, mature vegetation, almost any plant may become established upon it. "Preparation" by pioneers for the shrub stage, and by that for the forest, is unnecessary. Shrubs and trees will develop on equal terms for a time, gradually eliminating the herbs. The trees will outgrow the shrubs and bring about their disappearance, and, with development of a normal forest undergrowth, establishment of the climax is attained.

Very different is the manner in which the upper reaches of Glacier Bay are being colonized. Rapid and continuous ice recession has bared enormous areas, in which a small group of species establishes a sparse but homogeneous population. These increase steadily in number of individuals, but new species are added very slowly. The three successional stages, pioneers, willow-alder thicket and forest, find opportunity for full development and appear conspicuously in reverse order as one travels up the bay. It seems that in long-range invasion the composition of the pioneer group is determined not by unusual ability to survive hard conditions but merely by possession of disseminules adapted for transportation by wind. An occasional seed of shrub or tree that in some way is carried to the vicinity of the far-distant ice finds no difficulty in germinating and developing into a healthy plant.

UNAKWIK INLET

This, the next major indentation west of Columbia Bay, is a typical fiord with a north-south axis, practically straight for 20 miles, bending sharply to the east near its head (Fig. 1). A mile and a half beyond the bend it is terminated by the active tidal cliff of the Meares Glacier. The bounding slopes of the upper third of the inlet are very steep, with fine hanging valleys and a number of minor glaciers.

The known history of the Meares Glacier is very uncertain. Fidalgo (see Davidson, 1904) first saw it in 1790, but was frightened away by the commotion it made. Vancouver entered the inlet in 1794, found it "much encumbered with ice," but did not reach its head. Glenn (1899) made the following surprising report for the year 1898: "When we arrived at the head of this inlet we found it divided into arms, both of which were frozen over. . . . We were unable, therefore, . . . to examine the glaciers that lay at the heads of the two arms." Grant and Higgins (1910-11) found in 1905 a *single* glacier front at a point a mile and a half below the junction of two major ice streams. Steady but slow advance followed as shown by the observations of Grant and Higgins (1913) in 1909, Tarr and Martin (1914) in 1910, and Field (1932) in 1931. Observations in 1935 revealed no perceptible change during the preceding 4 years.

If one is to accept Glenn's rather circumstantial account, coalescence of two ice streams into one and advance of 2 miles occurred between 1898 and 1905. This is not in itself unreasonable, but the subsequent behavior does not agree with that of other

FIG. 8. Miscellaneous pioneer vegetation on moraine vacated by Columbia Glacier shortly after 1914. In distance, forest invaded by recent advance of ice. Locality A, Fig. 7.

Alaskan glaciers that have made sudden advances, which almost immediately begin a slow but definite recession. Recent cessation of advance may, however, be preparatory to a phase of shrinkage, and the future history of the glacier will be watched with interest.

The slopes are well forested throughout the length of the fiord. Timberline descends gradually from 1,500 feet to about 1,000 feet at the glacier front. At the bend there is a striking relation, noted also by Tarr and Martin, between the forested areas and the hanging valleys. Below the lips of the latter there is dense forest, but none at the bases of the high intervening ridges. Avalanching is the obvious answer. There is little forest on the slopes south of the glacier above the terminus, but on the north side it extends beyond the ice cliff in a narrowing wedge for at least 2 miles. Its lower edge is in practical contact with the glacier surface. Conditions here agree with those in Columbia Bay. The forest evidence proves that the ice is as far advanced as it has been for centuries; the wedge of super-glacial forest suggests destruction of vegetation below it by advancing ice. If Glenn's account may be trusted, much of this happened between 1898 and 1905. A careful examination of the ice-forest contact should throw light on the problem.

Passage Canal

Passage Canal (Fig. 12), a fiord 12 miles long and 2 miles wide, is continued westward by a through valley opening to the head of Turnagain Arm of Cook Inlet. The vegetation is reminiscent of Unakwik Inlet. Both sides bear mature forest, in which mountain hemlock is vastly preponderant, from sea level to timberline at 700-1,000 feet. On the north slope, which is higher and steeper, the forest is much cut by avalanche tracks, so that in many places mere strips of trees are left. The broader tracks are filled with alder thicket; the narrower ones, where avalanche action is more concentrated, support only herbs and small shrubs. On the gentler south slope the forest is far more continuous, and considerable areas of tundra occur.

College Fiord

The remaining three fiords are characterized by reduction of forest to small patches and great extent of alder thicket and other non-forest vegetation.

College Fiord continues the main axis of Port Wells northeastward 27 miles (Figs. 1, 9). At its extreme head is the ice cliff of the Harvard Glacier. Five miles below, Yale Arm, terminated by the Yale Glacier, enters from the east at an acute angle. The main range of the Chugach Mountains lies northwest of the fiord, its highest peak, Mt. St. Agnes (13,250 ft.), being only 12 miles distant from the Harvard ice cliff. From the southeast flank of the range descend several remarkable cascading glaciers, four of which reach tidewater. These are the Wellesley, Vassar, Bryn Mawr, and Smith. Several others of equal size farther northeast are tributary to the Harvard. Scores of smaller glaciers lie upon the steep slopes of the lofty Chugach Range and the lower mountains on the opposite side.

Vancouver penetrated the fiord far enough to see and hear the iceberg discharges from the glaciers at its head, but there are no reliable accounts of conditions there until the visit of the Harriman Expedition in 1899. From then to 1935 the Harvard Glacier steadily advanced, the total distance gained being about 2,000 feet. The Yale has had a similar recent history. The four cascading glaciers also advanced after 1899, but not so consistently; the fronts of all were in 1935 behind the maxima reached a few years before. The smaller glaciers seem for the most part to have receded or undergone no noticeable change.

The slopes along lower College Fiord are mantled with forest accompanied by the usual heath. On the southeast side the forest is fairly continuous almost to the mouth of Yale Arm; beyond, it is much broken by avalanche tracks. The southeast side of Harvard Arm has a strip of mature forest along the shore for 2 miles, and patches similar in nature follow the ascending ridge top almost to 2,000 feet. Farther northeast the forest is much broken, but small groups and isolated trees extend a short distance beyond the ice cliff. On the northwest side of the fiord continuous forest extends only 5 miles above the mouth. Beyond, it is very patchy, and from a point 2 miles below the Wellesley Glacier to the Harvard ice cliff, trees occur only in small groups or individually, though these are distributed from sea level to an altitude of more than 1,500 feet. There is far less forest on this side than on the other.

The tree groups give every appearance of great age. There are usually a few large spruces, up to 3 feet in diameter, and more numerous, smaller hemlocks, which are probably as old as the spruces. Standing dead trunks and rotten stumps are common. At the west end of the Harvard cliff (A, Fig. 9) a spruce that had barely escaped destruction by advancing ice just before 1935, 50 feet tall and 28 inches in diameter, showed 246 growth rings. The forest-thicket complex at this point is therefore more than two and a half centuries old, and the ice has not been farther forward for at least that length of time.

The unforested portions of the slopes on both sides of the fiord are occupied principally by alder thicket up to an altitude of nearly 2,000 feet. It fills the avalanche tracks, and along the northern half of the northwest shore it forms an almost complete mantle (Fig. 10). At Glacier Bay alder thicket is evidence of successional immaturity. Here (except in Yale Arm, to be considered shortly) there is no reason to assume that as a type it is significantly younger than the forest patches associated with it. The individual stems are, of course, short-lived, but vegetative reproduction is going on constantly as well as reseeding.

In spite of its lack of homogeneity, the vegetation as a whole seems to be essentially in equilibrium with its complex environment.

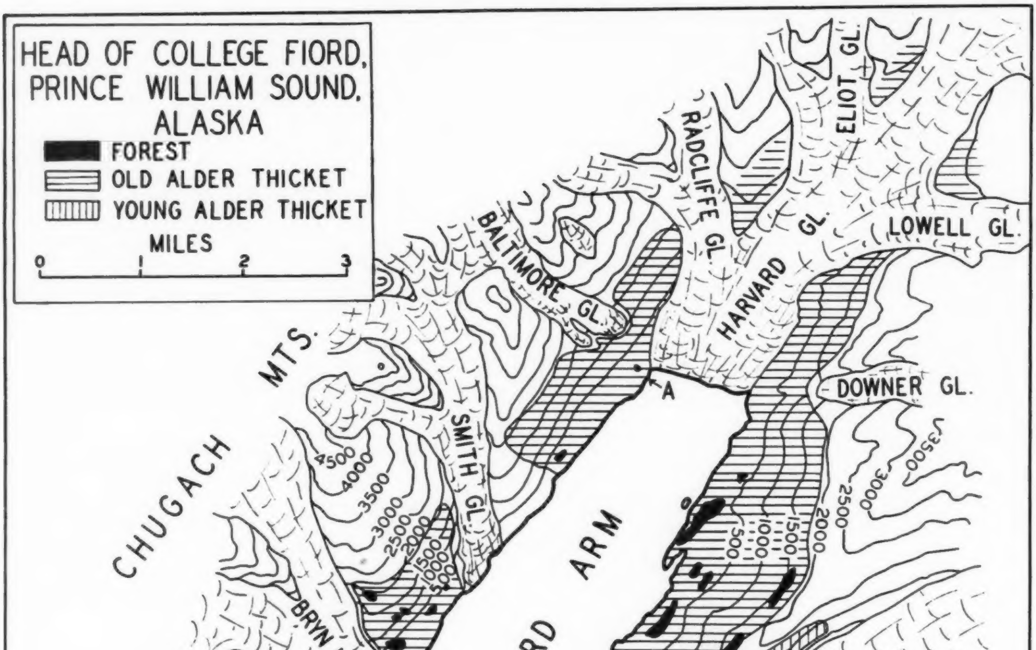


FIG. 9. Map of upper portion of College Fiord.

The alder thicket continues beyond the ice cliff of the Harvard Glacier on both sides, and patches occur on the promontories between the cascading tributaries at least 4 miles above the terminus. Here again, as at Columbia Bay and Unakwik Inlet, mature vegetation at the ice cliff and above the glacier surface (even though it is mainly alder thicket instead of forest) strongly suggests destruction of similar vegetation on the lower slopes by advancing ice.

In Yale Arm there is evidence of an event unusual in this region—rather pronounced retreat of a trunk glacier long enough ago to permit development of the alder thicket stage in the normal successional series. The terminus of the Yale Glacier stood, not

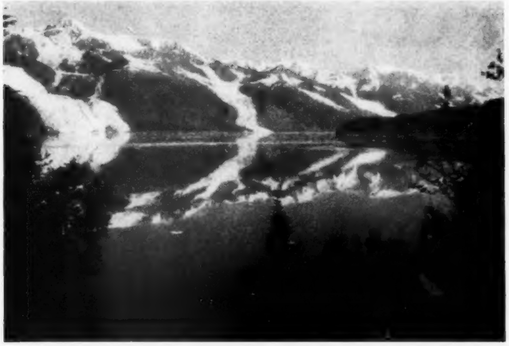


FIG. 10. College Fiord, looking northwest from near mouth of Yale Arm. College Point at right. Left to right on far shore, Bryn Mawr, Smith and Baltimore Glaciers. Lower slopes between them clothed mainly with alder thicket.

long ago, at the mouth of Yale Arm, 2 miles in advance of its present position. The evidence for this is found in the presence of strips of youthful vegetation (B, C, Fig. 9), beginning at sea level on College Point and the shore opposite and extending to the ice cliff and above the ice surface a short distance beyond. On the southeast side the lower limit of the mature forest-thicket complex, opposite the ice cliff, stands at about 700 feet. Below it is a fringe of young trees, then dense *young* alder thicket to the shore, with occasional young spruces. On the northwest side the widening belt of youthful thicket may be seen rising to a height of 1,500 feet a mile beyond the terminus. Above it, crowning the ridge, is the mature forest, undisturbed for centuries. In its current readvance, the glacier has invaded the younger vegetation and destroyed a portion of it. Tarr and Martin (1914, pp. 308, 314), who realized the significance of the vegetational evidence here, found a 33-year-old willow at the edge of the advancing ice in 1910, which sets a minimum length at that point for this very minor and probably local phase of contraction.

HARRIMAN FIORD

When the Harriman Alaska Expedition in 1899 sailed up Barry Arm to obtain a close view of Barry Glacier, which apparently terminated the inlet, they discovered an opening between ice cliff and western shore leading into an unknown fiord which they named for the sponsor and leader of the expedition. Harriman Fiord (Fig. 1) is 12 miles long. The main range of the Chugach Mountains, here from 7,000 to nearly 10,000 feet in height, lies parallel to it on the northwest, and lower but glacier-crowned mountains on the southeast. The principal tidewater glaciers are the Barry, at the northeast angle, the Serpentine, barely touching salt water, the Surprise, heading a short side arm, and the Harriman, at the head of the fiord. Several cascading glaciers, resembling those of College Fiord, reach tide level or come close to it, and the upper slopes are largely sheathed with ice.

The recorded history is obviously a brief one. The Barry Glacier seems to have reached its recent maximum in 1898 (Tarr and Martin, 1914, p. 322). In 1899 it completely occupied its own inlet, and a huge peninsula of ice extended to within three quarters of a mile of the opposite shore. Between 1899 and 1914 its front receded $3\frac{1}{2}$ miles; since then, up to 1935, there has been no further significant change. The Serpentine has receded half a mile, the Surprise a mile and a quarter. The Harriman, following a slight recession between 1899 and 1909, has advanced steadily, gaining more than 1,600 feet up to 1935. The smaller glaciers have had varied histories, with few notable changes. The margins of all the glaciers except the Harriman were in 1935 behind the lines of their recent maxima.

The vegetation is similar to that of College Fiord. There is considerable forest on the southeast side to a point opposite Surprise Glacier (Fig. 2); beyond, scattered patches occur almost to the Harriman Glacier. On the northwest side the slopes, except in the vicinity of the Barry Glacier, are almost treeless. Alder thicket is extensive on both slopes, but does not form so complete a cover as in College Fiord. Areas of loose slide rock support a rank growth of herbs and shrubs. At the sides of the Harriman Glacier the dominating type is a variation of the heath mat, in which Harrimanella, Nephrophyllidium and Lutkea dominate. The edge of the ice in 1935 was plowing into this, throwing up the peaty turf into folds (Fig. 11).

FIG. 11. Flank of Harriman Glacier, in its expansion pushing up turf of heath mat into folds.

The vegetation in Harriman Fiord is very ancient. In the tree group nearest the glacier four hemlocks from 6 to 9 inches in diameter were bored; these had 308, 208, 195, and 194 rings, respectively. Trees twice as thick were present, but defied penetration by the auger. Muir (1902, p. 133) counted 325 rings on a hemlock stump 9 inches in diameter "well up toward the head" of the fiord. Here, as in College Fiord, the vegetation seems to be in equilibrium with its environment. Gilbert, of the Harriman Expedition, recognized this (1904, p. 96): "In other localities there has seemed good reason to ascribe absence

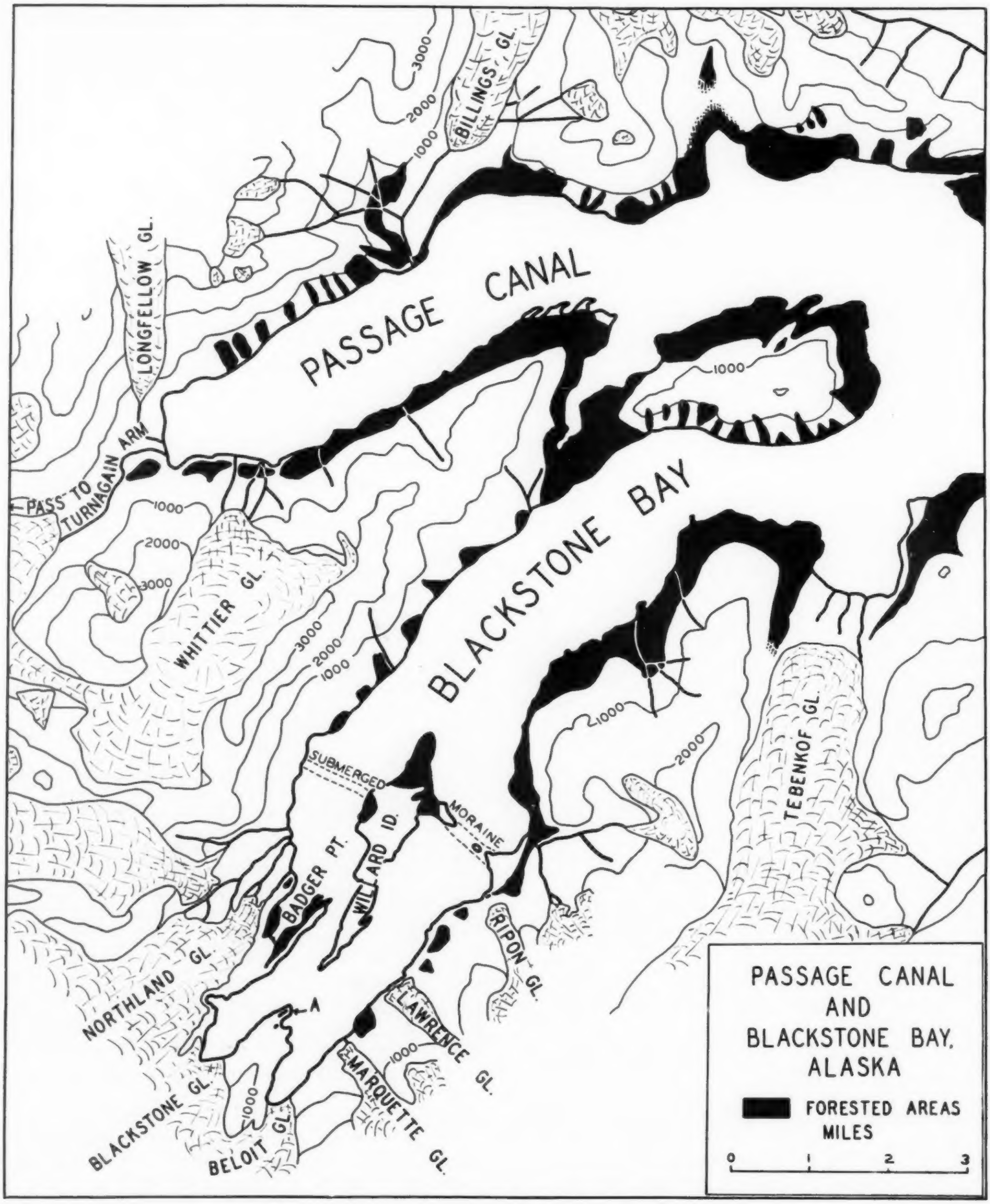


FIG. 12. Map of Passage Canal and Blackstone Bay.

of forest to recent occupation by ice, but here there is a sort of transition from forest to barren which suggests climatic limitation." Tarr and Martin (1914, p. 347) came to a similar conclusion: "This vegetation proves clearly that these fiords have not been occupied by brimming ice since at least the sixteenth century." They make the pertinent observation that "the presence or absence of trees and their size are not absolute criteria for use indiscriminately in interpreting glacial history." Use of the word "presence" should have been qualified. The presence of even a single living tree in undisturbed position is assuredly an absolute criterion for non-occurrence of glaciation at that spot during a period corresponding

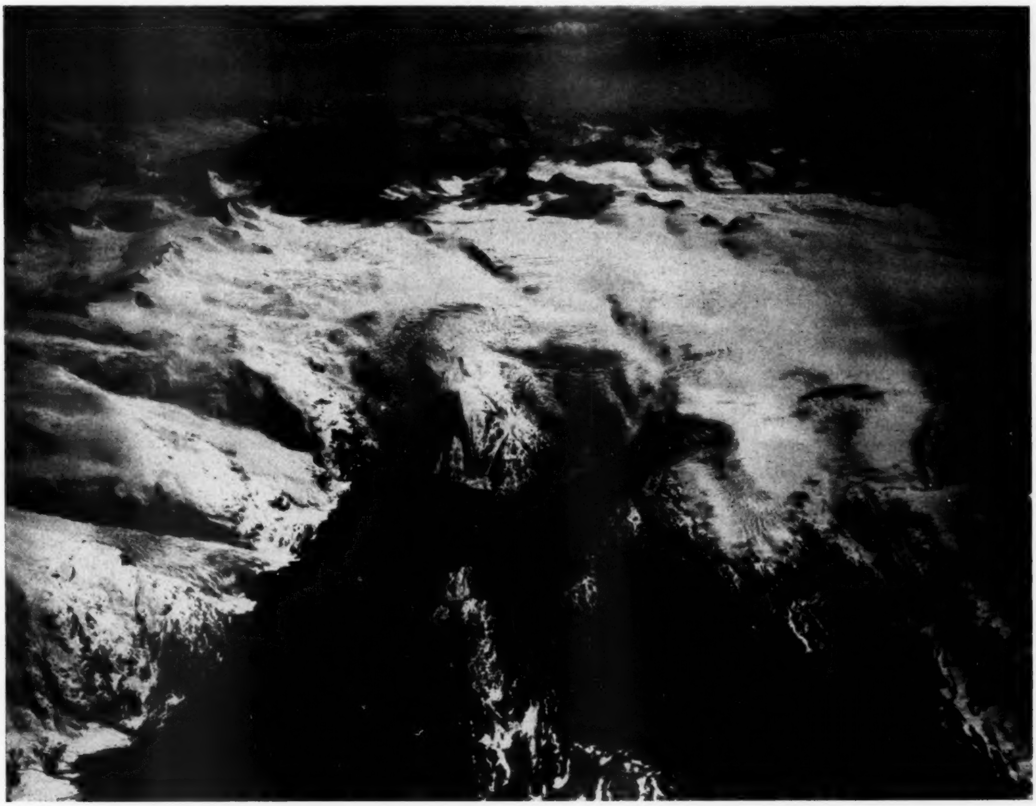
with the life span of that tree. It is plain, on the other hand, that absence of trees may not be used as a criterion of recent glacial recession, for other types of vegetation may be as ancient as any forest.

The recession of the Barry Glacier since 1898 and its preceding advance remind one of the similar performance of the Yale at a somewhat earlier date. The ground left bare by the retreat of the former is being invaded in normal fashion, and will soon be clothed with alder thicket and eventually by forest. The same is true on a lesser scale of the Surprise, the Serpentine, and the smaller, non-tidal Toboggan Glacier.

BLACKSTONE BAY

The mountains of the Kenai Peninsula must receive an amount of snow precipitation out of all proportion to their height. The summits range, on the average, from 5,000 to 6,000 feet, and yet the two great upland masses are brimming over with ice. Blackstone Bay (Figs. 12, 13) penetrates the northern edge of the eastern massif. Looking toward its head, one sees a gently undulating skyline of névé with a few peaks rising to a very moderate height above it. Two glacial outlets, the Blackstone and Beloit Glaciers, come steeply down to the head of the bay, discharging an abundance of icebergs. Three others from the east practically reach tidewater; those on the west are somewhat more distant. Willard Island and Badger Point are conspicuous features of the upper bay. The lower part is bounded by non-glaciated mountains 1,000 to 2,000 feet high. Tributary to Blackstone Bay near its mouth is the Tebenkof Glacier, a large non-tidal ice stream, which is so distinct in location and character from the others that separate treatment is desirable. Though earlier explorers had entered the bay, the first to describe its glacial features were Grant and Higgins (1913), who made a brief visit in 1909. Martin (Tarr and Martin, 1914) made investigations in 1910. Since then, up to 1935 (Field, 1937), it seems to have been entirely neglected by scientific visitors. With few human records to draw upon, the evidence of the vegetation assumes special importance.

The shores of Blackstone Bay near the mouth are forested like those of adjoining Passage Canal. There is further agreement in that the forest on the north side goes higher (to 1,000 feet) and is much cut by



Photograph by Bradford Washburn

FIG. 13. Head of Blackstone Bay from the northeast. Willard Island in foreground; Beloit and Blackstone Glaciers descending from snowfields of Kenai Peninsula. At the tip of the point between them (A, Fig. 12) grew the hemlock of Fig. 14.

avalanche tracks, while on the south slope these are scarce, and there is considerable tundra. Passing up the bay, the forest is gradually reduced to isolated patches alternating with the usual accompanying types. There is dense mature forest on the north end of Willard Island. The remainder is almost treeless in parts, with alder thicket, heath and Calamagrostis meadow dominating. Such trees as occur are comparatively small. Patches of mature forest occur on the east mainland shore between Ripon and Lawrence Glaciers. Badger Point is covered with a vegetation-complex of the usual type.

The most significant locality is the point which projects northeastward between the Blackstone and Beloit Glaciers (A, Fig. 12; Fig. 13). This bears heath, alder thicket, and groups of hemlocks. The largest of the trees, 50 feet high and 3 feet thick, was cut to the center and the rings counted and analyzed roughly. To its demonstrated age of 417 years must be added a period of time—reasonably 20 to 50 years—represented by an uncountable quarter-inch of radius at the center and height growth of 2 feet to the level of the cut. It is certain, therefore, that the ice has not been more than a mile forward in Blackstone Bay for at least four and a half centuries. The growth history of the tree as recorded by the rings (Fig. 14) is a normal one. After an

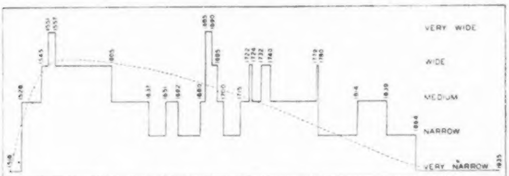


FIG. 14. Ring-history of hemlock which grew at A, Fig. 12. Description in text.

initial period of very slow growth a rapid increase in rate occurred which reached a maximum in 1551-1557. A gradual decline ensued, with the usual minor ups and downs, terminating in a long period of exceedingly slow growth correlated with maturity. The pronounced peak of 1685-1690 seems reasonably attributable to climatic causes. The freedom to develop normally which this tree has enjoyed throughout its life suggests that the two nearby glaciers have at no time crowded closely upon its vicinity.

Grant and Higgins (1913, p. 44) note the presence of a partially submerged moraine connecting Willard Island and the mainland on the east, and Tarr and Martin (1914, pp. 358-360) describe it in detail. The first authors noticed the dense forest on the north end of the island in contrast with the comparative poverty of the vegetation south of the general location of the moraine, and concluded that there is here mutually corroborative evidence, geological and botanical, that "perhaps two centuries ago the front of the Blackstone Glacier did extend well up to the north end of Willard Island." It did not escape them that the east side of the bay bears mature forest south of the moraine, but they explained this by assuming more rapid tree growth on the gravels along that shore. The forest patches here, however, occur on bedrock, not on gravels.

Tarr and Martin further elaborate the argument, speaking of Willard Island south of the moraine as a "somewhat overgrown barren zone." They regard the abrupt limit of forest apparently coinciding with the position of the moraine "not as a feature related either to climate or soil, but as clear proof of a maximum of the Blackstone, Beloit, and adjacent glaciers a century or two ago." This categorical statement seems inconsistent with their warning already quoted against indiscriminate use of tree evidence in interpreting glacial history. Their conclusion is disproved by a single ring count.

In 1935 an almost completely submerged moraine was found across the channel west of Willard Island corresponding with the one on the east (Field, 1937, Fig. 23). It seems certain, therefore, that at some earlier period the ice front did stand here for a time. The vegetational evidence, however, is deceptive. The forest on Willard Island lies for the most part to leeward of a high hilly mass, and in places extends southward beyond the line of the moraine. On the mainland shores there is no abrupt vegetational change corresponding with the moraines. The sparsity and smallness of tree growth on the southern part of the island is probably due to exposure to winds from the snowfields. The more numerous, larger, and older trees on Badger Point and between the two principal glaciers, though closer to the glacial sources, are sheltered by the abrupt slopes that rise just south of them. The stand of the Blackstone Bay glacier across the north end of Willard Island must be relegated to a period so remote that all vegetational evidence thereof has disappeared.

Tebenkof Glacier. This large ice stream, flowing in a valley parallel to upper Blackstone Bay, ends more than a mile back from the shore, and is fronted by moraines and outwash. In 1910 (Tarr and Martin, 1914) it was receding, and 12-year-old alders indicated that its recent maximum occurred before 1898—not long before, judging from the sparseness of pioneer growth. At that earlier time it was advancing into mature vegetation. The 1935 expedition found remnants of forest, with stumps in place, very recently uncovered by recession of the ice. Of 24 samples collected, 20 were hemlock and 4 spruce. This destruction is quite certainly of recent date, and not to be compared with the buried forest remnants of Glacier Bay.

THE CLIMAX IN THE FIORDS

All six fiords here described agree in supporting upon their slopes, practically to their heads, mature vegetation of some sort. In other words, there is not, as at Glacier Bay, a transition headward from forest through willow-alder thicket to pioneers. The six fall, however, as already noted, into two groups of three each. Columbia Bay, Unakwik Inlet and Passage Canal are alike in displaying the forest-tundra complex normal to the general region. In College and Harriman Fiords and Blackstone Bay

the forest is gradually reduced headward to patches which become smaller and smaller (though not demonstrably younger); as forest diminishes alder thicket becomes dominant.

These two groups differ markedly in the amount and character of nearby glaciation. The fiords of the first group are far less hemmed in by glacial masses than are the others. The slopes around Columbia Bay bear no glaciers. The Columbia Glacier itself is very large, but the short, broad bay lies open to oceanic influences and the concentration of down-draft from the ice fields is minimized. Unakwik Inlet is terminated by a trunk glacier, but this lies around a sharp bend. Glaciation of surrounding slopes is moderate. Passage Canal has no glaciers that reach tidewater, and the trough that is its headward continuation opens out to the waters of Cook Inlet, so that conditions producing frigid down-draft are absent.

The fiords of the second group penetrate deeply into high mountain masses heavily laden with snow. Cascading glaciers descend in many places to the water's edge, and the high intervening mountain shoulders are largely sheathed with ice. Moreover, all have trunk glaciers occupying great troughs which concentrate the currents of cold air from the névé fields and lead them down to the fiords. The axis of the Harvard Glacier is continuous with that of College Fiord; the Yale enters at an acute angle. Harriman Fiord has four major glacier-filled troughs converging upon it. Blackstone Bay has several short steep ones descending from an extensive névé.

It seems a reasonable supposition that local climatic conditions are more severe in the second group of fiords, since the influence of the surrounding ice fields must be carried down within them even to sea level. Climatic data presented in an earlier section somewhat indirectly support this assumption. Valdez, with a relatively severe climate, is representative of the glacier-hemmed fiords of the second group. Cordova, the contrasting station, lies near the open coast. The fiords of the first group, farther inland than Cordova and bounded by high abrupt slopes, but less subject to glacial influences than Valdez, should logically have climatic conditions intermediate between the two in severity.

Granting a real difference in climate, it is natural to accept this as an explanation of the striking difference in vegetation, and to consider the vegetation of the ice-surrounded fiords as a local climatic climax. The qualification must be made, however, that nowhere is the climate so severe as to exclude trees absolutely; hemlocks of fair size and great age occur here and there even to the immediate vicinity of the ice fronts.

Another factor—avalanching—must be considered as a probable deterrent to forest development. The abundance of alder thicket, a characteristic type in avalanche tracks throughout the Pacific northwest, indicates this. One is tempted at first thought to simplify the cause by recognition of the obvious fact that avalanching depends upon abundant snow precipitation. It might therefore be considered as an agency through which climate acts upon vegetation. Unfortunately for this viewpoint, the snow which becomes an avalanche is brought to the lower slopes by gravity from a quite different climatic zone, in which snow precipitation is very much greater than at sea level.

The question, whether or not the distinctive vegetation of the ice-bounded fiords constitutes a local climatic climax, is perhaps an academic one. The fundamental facts, at any rate, seem clear. The vegetation is in approximately stable adjustment with its environment and has existed essentially as it is today for at least several centuries. While there is notable decrease headward in amount of forest, there is no indication of decreasing vegetational maturity. In this respect it is uniform all the way to the sharply cut boundary that indicates the high-ice mark of recent or current glacial advance.

AN EXCURSION INTO POSTGLACIAL CLIMATIC HISTORY

That sharp line of demarcation, with a narrow barren zone or the ice itself on one side and uniformly mature vegetation on the other, is of the utmost significance with regard to the glacial history of the last half thousand years, and possibly for a much longer period. It is proof that, in the area covered by the present investigation, the ice is today essentially at flood. In certain places the glaciers are encroaching upon ancient vegetation. In others they have shrunk away from the line of greatest advance, but the amount of shrinkage has in most cases been insignificant, and nowhere more than $3\frac{1}{2}$ miles. Recession, rapid for a time, has often been succeeded by quiescence or renewed advance. At most points the period since shrinkage began is demonstrably a matter of a few decades; in no known case is it more than about a century.

The same sharp line of demarcation is evident everywhere in coastal Alaska where glaciers enter the zone of forests. In certain places conditions parallel those at Prince William Sound; for example along the west slope of the Fairweather Range, where the ice is at flood, cutting into mature vegetation or having very recently done so. In other areas, and particularly along the mainland coast behind the Alexander Archipelago, the ice edge in a majority of cases lies much farther back from the ancient forest margin. Here there has been opportunity for development of the characteristic successional stages: young climax next to the ancient forest (but sharply distinguished from it), willow-alder thicket next, and pioneers nearest the ice. It seems clear that in these parts an important maximum occurred a century and a half or two centuries ago, and was followed by widespread and consistent recession. There have thus been regional differences in time of culmination, rather large from the human viewpoint, as well as local ones on a minor scale. Nowhere, so far as present evidence shows, may the

maximum be placed more than two centuries ago; nowhere has the sharpness of the forest margin been blurred.

Such a maximum implies a preceding period of contraction. As to the magnitude of this, in space and in time, Prince William Sound offers little evidence. The age of the oldest trees in close proximity to the edge (250-450 years) denotes several centuries at least during which the ice was less advanced than now, and the general aspect of the vegetation indicates great age.

There is, however, pertinent evidence from Glacier Bay. Here the remains of buried forest of fully developed climax character have been uncovered 45 miles back from the line of farthest recent advance (Cooper, 1923, 1931A, 1939A). The oldest tree discovered in these deposits had 480 rings; other evidence described in the papers cited justifies doubling this for a minimum estimate of the life of the forest at this point. Since the forest grew there, subsidence of at least 20 feet has taken place, proved by stumps found in place extending down to the level of low tide (Cooper, 1923, p. 107).

It is quite true that caution must be used in gauging events in general by what happens at Glacier Bay. I have previously pointed out (1937, p. 61) that that area has been exceptional in the magnitude and rapidity of the recent ice recession, and that the preceding advance may also have been out of line with the average for the region. But, making all reasonable allowance for its uniqueness, the evidence of the lengthy period of forest growth so far within the limits of the recent maximum, together with the time required for subsidence during the period following, seems to compel the assumption of a period since the establishment of the ancient forest rated in terms of millennia.[2]

From the observations of Tarr and Martin (1914) it appears that Yakutat Bay has had a post-Pleistocene history quite similar to that of Glacier Bay. There is even evidence of a period of glacial contraction during which forests developed at least as far up the fiords as the position of the present ice fronts.

The magnitude of these events, in space and time, indicates as a cause a considerable climatic pulsation, which must have affected the behavior of glaciers throughout coastal Alaska, including those of Prince William Sound, though not necessarily on so vast a scale as at Glacier Bay. I expressed this belief in a previous publication (1937) which dealt solely with Glacier Bay, but went no farther at that time.

An extension of this thought now seems justified. The hypothesis is offered that the "present" in coastal Alaska (comprising the last few centuries and extending into the future) is a time of ice expansion on a scale not equalled during very many centuries of the past. It is true that recession is now the dominating process—that it has been in progress in some places for two centuries. On the other hand, in a rather important minority of cases, the ice is now actually at flood. From the human viewpoint 200 years seems a long time, but it is manifestly too short a period from which to judge the significance of present trends of advance or retreat. The ratio between two centuries and the total time since the peak of the last Wisconsin ice-flood (40,000 years) is but 1:200. It is quite reasonable to assume that the high-ice mark of 200 years ago at one point, and of today at another, represent a single major maximum, reaching its crest in different places at slightly different times.

Associated with this hypothesis is the suggestion that the preceding period of contraction was of a magnitude so great as to make it the major event of mid-post-Pleistocene time; in other words, that it corresponds with the warm middle period of Von Post, or with the lengthy warm period of the Blytt-Sernander scheme, which is assumed to have embraced both dry and moist phases.

These two hypotheses have been based largely upon peat and pollen studies of European material. The majority of American workers seem at the present time to be inclined toward acceptance of Von Post's interpretation. A few hold with neither, feeling that, while there is convincing evidence of a shift of climate from glacial to postglacial, there is none of positive nature bearing upon possible major postglacial pulsations.[3] My own view is that the disappearance or extreme reduction of spruce, shown so consistently in pollen profiles of northern bogs, and its reappearance or marked increase at the top of the column, indicate northward recession of this species followed by southward advance; with the added inference that middle post-Pleistocene time was characterized by a maximum of warmth which was followed by a period of lower temperatures extending to the present.

The problem has been attacked also by certain phytogeographers, who find evidence in vegetational studies for a period warmer (or drier, or both) than now, covering some portion of post-Pleistocene time; or they feel that such an assumption is helpful in attempting to solve certain knotty phytogeographic problems (Porsild, 1922; Gleason, 1922; Transeau, 1935; Raup, 1937; Abbe, 1936, 1938).

Ranging still farther afield, there is abundant nonbotanical evidence of various kinds. Since this may be unfamiliar to many ecologists, it seems worth while

[2] I wish to take this opportunity to correct a misinterpretation of my conclusions as to the age of the "interglacial" forest of Glacier Bay, which appears in a recent paper by Dr. Griggs (1934A). On page 94 there is the following statement: "The peat [on Kodiak Island] does not therefore carry us back into the period of the fossil forest discovered by Cooper (1923), around Glacier Bay. Here an old forest was buried under many feet of gravels deposited during the last glaciation. These forests would seem to represent interglacial time in contrast to the postglacial history with which we are concerned at Kodiak." The inference is that the forest grew during a pre-Wisconsin interval. My use of the word "interglacial" in a general sense, denoting a period of contraction between two pronounced maxima, was perhaps unfortunate. I feel, however, that in the paper referred to my meaning was made quite clear, and in a later one (1937) it is absolutely definite. The period of glacial contraction during which the forest grew was an event of *post-Pleistocene* time. The gravels, with the forest relics they contain, could never have survived the intense erosion which must have occurred during the Wisconsin ice-flood. The basal layers of the Kodiak bogs are probably older than the buried forests of Glacier Bay.

[3] For critical reviews of the entire problem see Sears (1935), Cain (1939), and Eiseley (1939).

to give here a summary account and evaluation of those studies which have come to my attention. In this survey there is no pretension to completeness. The contributions may be conveniently grouped as follows: glacial behavior in Alaska, history of lakes in the Great Basin, recent history of small glaciers in the western mountains, origin of ancient sand dunes and terraces, and geothermal gradient.

Alaska glacial studies. Certain geologists have come independently to interpretations similar to mine, and in some cases they have utilized vegetational as well as purely geological evidence. Wentworth and Ray (1936, pp. 932-933), considering certain glaciers distributed between Juneau and the Kenai Peninsula, offer the following synopsis of post-Pleistocene history:

"1. Great extension of glaciers in late Pleistocene time. . . .

"2. A period of several thousand years of net recession, . . . eventually reaching receded positions somewhat inland from those of 1931.

"3. Maintenance of receded position for several hundred years, permitting growth of spruce forests somewhat inland from those of 1931.

"4. Advance of glaciers, probably by some thousands of feet, so as to trim the spruce forest to the lines now clearly shown near many glaciers. Maximum position of advance probably not maintained for more than one or two decades, and the advance probably taking place within the past 200 years, for the spruce forest has not generally been completely reestablished inland from the aforementioned line.

"5. General recession during the past 100 to 200 years, doubtless with many unknown fluctuations." (Items 6 and 7 relate to minor changes since 1900).

That these authors recognize the importance of the sharply drawn forest edge is evident from the above quotation and from the following (*op. cit.*, p. 932):

"Existence of this sharp line is the chief evidence that at least once since Pleistocene time most of the glaciers retreated to positions probably inland from their present margins, permitting the advance of vegetation and the growth of mature spruce forests during perhaps 300 years, in positions not over 200 or 300 feet from the 1931 margin of the ice. Future exposures of overridden and buried forests may show that recession of far more marked character has taken place, but with present knowledge, one can carry the inference no further."

It would seem that Wentworth and Ray are unnecessarily conservative in their estimate of "some thousands of feet" of advance leading to the recent maximum. The evidence of the overridden forests of Glacier Bay seems to have been overlooked. Neither does their belief that the "maximum position of advance [was] probably not maintained for more than one or two decades" seem justified. The amount of material in the recent end-moraines of the Great Stikine, Davidson and Glacier Bay glaciers (to mention only those the writer has himself seen) indicates a far longer period.

Kerr (1936), treating the glaciation of the Coast Ranges of northern British Columbia and adjacent Alaska, also postulates an important period of ice contraction followed by a notable advance. Relying for evidence mainly upon the rate of filling of fiords by delta deposition, after they had been vacated by the ice, he estimates that the relatively warm (or dry) period which brought about contraction extended from about 5,500 to 1,500 years ago. He also suggests correlation with the assumed warm-dry period in Europe in middle post-Pleistocene time.

Hanson (1934) has drawn similar conclusions from similar sources of evidence. He estimates that the Bear River delta at the head of Portland Canal, at the southern boundary of Alaska, fed by streams from small mountain glaciers, required about 3,600 years for its formation. The glaciers which supply its materials must therefore be of comparatively recent origin and not remnants persisting from the Pleistocene; or, if they are, they must have been very small and inactive for several thousand years. "Over the period of the last 9,000 years, temperatures have been higher than those of the present for about 4,000 years and about the same as those of today during 5,000 years." He notes the presence of a clearly defined high-ice mark above the sides of the glaciers, and recent moraines as far as 1 or 2 miles below their present ends.

Saline lakes of the Great Basin. A number of the lakes of the Great Basin, repositories of interior drainage, are only moderately saline. Gale (1915) calculated that accumulation of the salt contained in Owens Lake, fed mainly by streams from the Sierras, must have required only about 4,000 years. Antevs (1938) interprets this to mean that the earlier and much larger lake of Pleistocene time dried up completely during the warm-dry period of middle post-Pleistocene time and was reborn when precipitation again increased and temperatures became lower. He considers the warm age, or Middle Postpluvial, as covering roughly the period from 7,500 to 4,000 years ago. A similar history has been suggested by Van Winkle (1914) for two lakes in south-central Oregon, with again an estimated requirement of 4,000 years for the accumulation of the contained salt. It should be added that the history of the Great Basin lakes has been a field fruitful in controversy, and that interpretations differing from the above have been offered (*cf.* Huntington, 1925; Brooks, 1926, pp. 386-395).

Small glaciers of Sierras and Rocky Mountains. Matthes (1939 A, 1939 B, 1940), in addition to pointing out the significance of the above lacustrine studies, has revived an idea first suggested by Russell (1889): that the small glaciers of the Sierras are not direct remnants from the Pleistocene, but newly developed following the middle period of post-Pleistocene time when the Sierras are assumed to have been utterly bare of ice. He considers the rather massive, exceedingly fresh moraines lying directly in front of the glaciers today as strongly suggesting an origin several thousand years later than the moraines clear-

ly associated with earlier recession. He thinks, further, that the greater glaciers which have certainly persisted from the Pleistocene "now have far greater extent and volume than they had during the middle third of the post-Pleistocene interval, and accordingly it may well be said that we are living in an epoch of renewed but moderate glaciation—a 'little ice-age,' that already has lasted about 4,000 years."

Matthes intimates that if this course of events is true for the Sierras, the small glaciers of the central and southern Rockies must have had a similar history. A study of certain glacierets in the Front Range of Colorado (Ives, 1938), though far from conclusive in this respect, is at least suggestive.

Ancient dunes and terraces. In two recent publications (Cooper, 1935, 1938) I described ancient stabilized sand dunes in the Mississippi valley in Minnesota and assigned their formation to physiographic processes occurring probably in late Pleistocene or early post-Pleistocene time. I pointed out, however (1938, pp. 202-203), that, although the physiographic cause proposed is adequate without recourse to aridity, the immediate stimulus to dune building may have been the oncoming of a period of arid climate, and that the previous lowering of the water table due to down-cutting by streams may merely have provided conditions of soil favorable to sand removal. In other words, the building of the dunes may be fitted into a middle post-Pleistocene arid period without doing violence to any known facts. Van Royen (1936) has studied certain stream terraces of the central plains and thinks that "these, and other physiographic observations in this area, can be more reasonably explained by the occurrence of one, and probably two pronounced dry periods during the postglacial than by any climatic changes dating back to Wisconsin and pre-Wisconsin times."

Geothermal gradient. Hotchkiss and Ingersoll (1934) have attempted to discover the general course of postglacial climatic change through mathematical analysis of rock temperature readings in the very deep shaft of the Calumet and Heela mine in northern Michigan. Assuming that the effects of external temperature conditions are transmitted so slowly through the earth's crust that conditions existing thousands of years ago are still measurable at depths of a few thousand feet, they find indications that the time of low temperatures associated with the decline of the last ice sheet was followed "by a period distinctly warmer than the present, which was succeeded in turn by one slightly cooler and lasting until rather recent time."

The foregoing survey indicates that there is a constantly growing mass of evidence derived from a number of fields of research, ranging over a large part of North America, and, quite naturally, varying in definiteness, which points toward the occurrence of a notably warm or warm-dry period in middle post-Pleistocene time. Its weight lies not so much in the value of individual contributions as in their mutual support. No one is decisive; combined, their testimony is impressive.

SUMMARY

Prince William Sound is a major indentation of the south coast of Alaska, with numerous tributary fiords which penetrate deeply the heavily glaciated surrounding mountains. During Wisconsin time the area of the Sound was occupied by a great piedmont glacier; today the ice reaches tidewater only in certain of the inner fiords. The climate in general is oceanic, with moderate, rather even temperature, and heavy precipitation, most of which, at sea level, is in the form of rain. In the inner fiords the climate is definitely less oceanic in character, with greater temperature extremes and far less precipitation, a larger percentage falling as snow.

The vegetational climax is essentially an extension of that of southeastern Alaska, with certain modifications. On the outer islands the forest is normal for the immediate coast. Sitka spruce (*Picea sitchensis*) dominates, and western hemlock (*Tsuga heterophylla*) and mountain hemlock (*T. mertensiana*) are also important. On the mainland shores north and west of the Sound, however, mountain hemlock is overwhelmingly preponderant. Sitka spruce is comparatively infrequent, and coast hemlock is almost absent. Another difference from the climax of southeastern Alaska lies in the abundant presence of areas of "tundra," which shows two intergrading phases, Empetrum heath and Carex bog. The first occupies relatively well drained localities, and is dominated by crowberry (*Empetrum nigrum*) and several dwarf heath-shrubs. The second is found mainly in areas of poor drainage, though sometimes in step-like arrangement on gentle slopes. The bulk of the vegetation is made up of sedges; Sphagnum is present in considerable abundance. Forest, heath, and bog are in fairly stable adjustment with environment, and it seems logical to consider the entire complex as a transitional climax between forest and tundra.

The major fiords fall into two classes. In the first, the walls are clothed with forest-tundra vegetation essentially like that of the open shores; in the second, forest is reduced to small patches, and alder thicket is the most conspicuous type. The two groups differ markedly in amount and character of nearby glaciation. Those of the second, which penetrate deeply into high mountain masses, are far more under the influence of great glaciers and extensive snow fields. It seems a reasonable assumption that local climate is more severe in the second group, and that the vegetational differences may be due, in part at least, to this fact. Abundant avalanching, however, may be a contributing factor. Whether or not the vegetation of these fiords is to be considered a local climatic climax, it seems at any rate certain that it is in approximately stable equilibrium with environment and that it has existed essentially as it is today for at least several centuries.

Everywhere in the line of possible ice advance the mature vegetation of the fiord walls terminates abruptly. Between this boundary and the glacier front lies a "barren zone," usually very narrow; or else

the ice is actually invading the ancient forest or tundra. The same sharp limit is evident throughout coastal Alaska wherever glaciers enter the zone of forest. At Glacier Bay and other localities in southeastern Alaska there has been ice recession for a period up to two centuries, but nowhere has the sharpness of the ancient forest line been blurred. Again at Glacier Bay, and at other points in southeastern Alaska, there is evidence that preceding the recent maximum indicated by the sharply cut forest border there occurred a period of contraction which endured for many centuries.

The hypothesis is offered that the "present" (liberally construed) in coastal Alaska is a time of ice expansion on a scale not equalled during many centuries of the past; that the high-ice mark of 200 years ago at one point, and of today at another, represent a single major maximum, reaching its crest in different places at slightly different times. It is further suggested that the preceding period of contraction was of a magnitude so great as to be a major, or perhaps *the* major event of middle post-Pleistocene time; that it corresponds with the warm or warm-dry (xerothermic) period first suggested by European students, accepted by a majority of American specialists in pollen analysis, and supported by other evidence derived from varied fields of research.

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HISTORY OF THE NATIVE VEGETATION OF WESTERN KANSAS DURING SEVEN YEARS OF CONTINUOUS DROUGHT

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HISTORY OF THE NATIVE VEGETATION OF WESTERN KANSAS DURING SEVEN YEARS OF CONTINUOUS DROUGHT*

INTRODUCTION

When the pioneers came from the East to make new homes in the Great Plains region, they found a dense cover of native vegetation. It was disturbed only by buffaloes, prairie dogs, other plains animals, Indians, and prairie fires. The Federal Government required that a certain amount of land be broken and put under cultivation, whether the land was obtained as a homestead or as a timber claim (McArdle and Costello, 1936).

The practice of the settlers was to break up a small tract of the prairie on which they could grow enough winter feed to sustain their cattle, horses, and other animals. The remainder was kept for pasture. Frequently the cultivated fields were cropped for a number of years and then abandoned to return to native prairie. Then the pioneers broke up and put under cultivation other similar areas (Clements and Chaney, 1937).

As the number of settlers increased and the demand for small grains, corn and sorghum became greater, additional acres were put under the plow. Agriculture approached stability with the growing of grain and forage crops incidental to the production of livestock. With the introduction of labor-saving machinery, it became possible for more land to be cultivated with even less manpower. This stimulated more extensive crop production. Even with the increased demands for farm products, the native grassland still remained of great importance to the farmer who kept livestock to increase his income.

The native grasslands of the Great Plains region are exceedingly important to the economic well-being of the people of the midwest. It is estimated that at present there are approximately 100,000,000 acres of land under cultivation, as compared with 175,000,000 that remain unbroken (Great Plains Committee, 1936).

The high prices of wheat during and following the World War caused many farmers, as well as wheat-farming corporations, to break vast areas in western Kansas. In fact, immense areas that had previously been regarded as "too risky" for growing wheat were broken for crop production. It is estimated that 18,000,000 acres are now under cultivation. In comparison, only 11,000,000 acres of grassland remain. Until about 1930, there was an unlimited market for wheat. Many farmers amassed considerable wealth through an extensive use of this one-crop system (Shantz, 1911).

At the beginning of the past decade, however, the wheat market reached the saturation point, and the price was reduced to less than 30 cents per bushel. Even at this low price it was impossible to dispose of any great quantity. Another factor that changed the outlook of the farmers was the period of deficient rainfall that appeared early in the "thirties." As a consequence of this drought, it was impossible to produce adequate crops; hence, the increased need for more grassland. But since the amount of the range land could not be increased in proportion to the demand, overgrazing resulted. This, in turn, led to a breakdown of the prairies. As cultivation continued despite the decreased rainfall, the soil became more pulverized, less porous, and more susceptible to erosion both by wind and water. Runoff was increased many fold, and the rate of erosion was accelerated enormously. One dashing shower sometimes removed as much as an inch of fertile soil, an amount which is produced naturally over a period of several hundred years (McDonald, 1938; Bennett, 1939). Dust storms which have occurred on the Great Plains since 1934 have been of unprecedented extent and intensity (Brandon and Kezer, 1936).

Just when the raising of cultivated crops became less important and the need for good pastures much more so, the combined effects of drought, dust, and overgrazing reduced the yield of vast areas of grasslands in the Great Plains region to almost nil.

TIME, METHOD, AND SCOPE OF STUDY

Studies of environmental factors and the reactions of vegetation were begun at Hays, Kansas, in 1931, before the drought. They have been continued almost uninterruptedly to the present time. Available soil moisture, measured throughout each growing season, has been found to be the most important factor of the environment of the plant. Precipitation, temperature, wind movement, and evaporation, also regularly measured, influence vegetation primarily through their effect upon the water supply or its loss. Permanent meter quadrats were extensively employed in obtaining quantitative data pertaining to plant reactions. In charting them, the pantograph was used, and the planimeter was employed in measuring the areas occupied by various species.[1] Numerous quadrats were staked out in 1932 and others subsequently, and each has been charted annually. Other methods of study were used, such as list quadrats, belt transects, and bisects. Field notes were extensively taken over wide areas. The area studied extends from Phillipsburg, near the northern edge of Kansas, through Hays, and to the southwest as

* This study was made with the aid of a grant from the Penrose Fund of the American Philosophical Society.

[1] Areas too small to be measured accurately by the planimeter were determined by superimposing circles of known area, inscribed on tracing paper or other transparent material, upon those of the charted quadrat sheet.

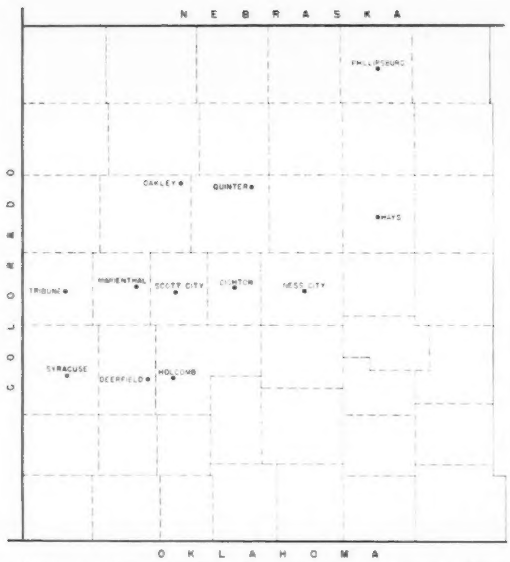

Fig. 1. Map showing the stations in Kansas where studies were made. These investigations have been continued since 1923 at Phillipsburg. They were initiated at Hays in 1931, and at the other stations in 1937.

far as Syracuse (Fig. 1). This work is a continuation of earlier studies by the authors (Weaver, 1924; Weaver and Albertson, 1936, 1939) and is supplemented by two related studies made in 1940 (Weaver and Albertson, 1940, 1940a).

ENVIRONMENTAL FACTORS

The average annual precipitation at Hays, Kansas, was approximately 5 inches above the normal (22.9 inches) during the 6 years (1927-1932) preceding the drought. Other environmental factors were likewise more conducive than usual to the growth of native prairie plants. Prairies moderately grazed were in excellent condition, but those that were ungrazed accumulated so much debris that the basal cover afforded by living plants was greatly reduced. The more mesic vegetation advanced up the slopes from the moist ravines and lowlands to the more xeric hillsides and tablelands. Big bluestem *(Andropogon furcatus)*, for example, which normally grows in ravines, was found in considerable quantities in the depressions or "buffalo wallows" on the nearly level uplands in 1932, at the end of the wet period. Little bluestem *(Andropogon scoparius)* and the wire grasses *(Aristida purpurea* and *A. longiseta)* likewise spread from their strongholds on the hillsides into the short-grass areas of the level uplands. It was not uncommon to find scattered bunches of these throughout the short-grass type. In general, plant production was somewhat above normal, and this luxuriance of growth made the vegetation more susceptible to the drought that followed (Clements, 1929).

The low rainfall during the dry years was accompanied by low relative humidity, high temperature, high wind velocity, and extremely high rates of evaporation. The damaging effect of insufficient precipitation was intensified by the fact that during the warm season, when soil moisture was most essential to growth, precipitation was often much less than normal.

Precipitation

The annual precipitation for the drought period during which this study was made (1933-1939) was below normal for every year (Fig. 2).[2] Only 3 of

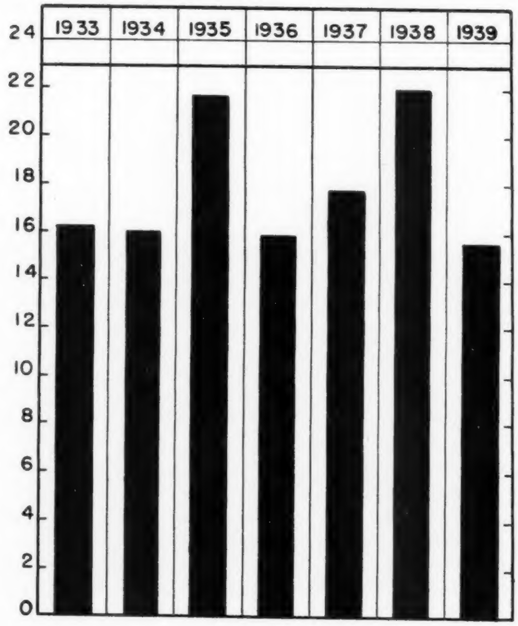

Fig. 2. Total precipitation in inches at Hays, Kansas, for 1933 to 1939, inclusive, and mean annual precipitation (heavy horizontal line).

the 7 years even closely approached normal, and during one of these 3 (1937) there was over 5 inches deficit. The remaining 4 years (1933, 1934, 1936, and 1939) each had approximately 16 inches, which is nearly 7 inches below normal.

Precipitation of the growing season (April to September) has a greater effect in determining the survival or death of the vegetation than has total precipitation for the year. May was the only month in which precipitation averaged above normal for the entire period and this resulted from several unusually heavy rains during May of 1935, 1936, and 1938 (Fig. 3). During 3 of the 7 years, rainfall for May was far below normal. The value accrued from the surplus moisture was offset by extremely abnormal conditions before and following the rainy period. In 1935, for example, 7 weeks of plentiful rainfall

[2] Data on precipitation and temperature were secured from the U. S. Weather Bureau.

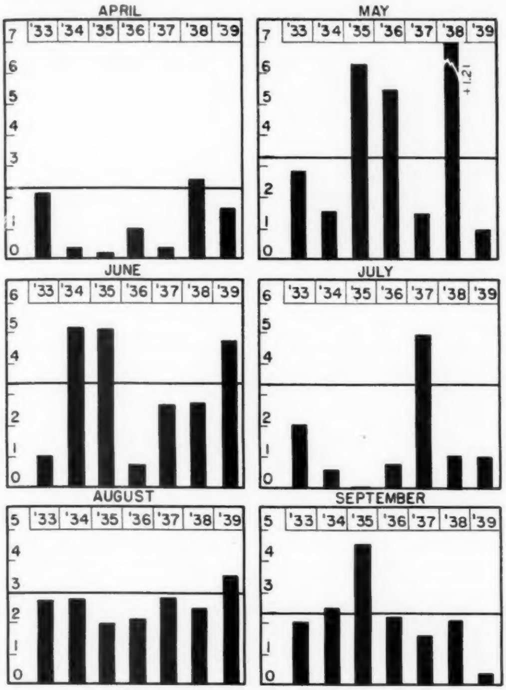

FIG. 3. Rainfall during each month of the growing season at Hays, Kansas, from 1933 to 1939, inclusive, and mean monthly rainfall (heavy horizontal lines).

during May and early June were preceded by the worst dust storms on record. The wet period was followed by one of equal length with scarcely any precipitation. It was during the month of July, 1935, that only 0.01 inch of rain fell. Rainfall for July, when soil moisture is indispensable to plant growth, averaged only 45 percent normal during the 7-year period. Only 2 years (1935 and 1938) had precipitation of about an inch or less below normal. Much of that in 1935 was lost because of the relatively impervious mantle of dust that was deposited over most of the soil and vegetation in March and April.

The total annual precipitation for the years 1933 to 1939, inclusive, was 34.46 inches below normal (Table 1). The amount received over a period of 7 years was approximately equal to what would be expected in 5½ years of normal precipitation. Furthermore, it was over 40 inches less than that received the 6 years previous to the beginning of the drought in 1933.

The accumulated deficit for the first 2 years of the drought (1933 and 1934) amounted to 13.5 inches. That during 1935 added only another inch, but this was followed by 2 years when the deficit was further augmented by over 12 inches, increasing the total to 26.6 inches. The precipitation for 1938 was only 0.8 inch below normal, but this resulted from an excess of nearly 5 inches in May. The deficiency for

TABLE 1. Mean monthly precipitation with departure from normal (1868-1939) and total departure each month (in inches), percent of normal precipitation for all years of each month, and accumulated deficits 1933 to 1939 at Hays, Kansas.

Month	Mean	1933	1934	1935	1936	1937	1938	1939	Total for each month	Percent of normal rainfall
Jan.	0.48	-0.41	- 0.19	- 0.48	- 0.33	+ 0.46	- 0.42	0.00	- 1.37	59
Feb.	0.84	-0.63	+ 0.32	- 0.56	- 0.64	- 0.45	- 0.19	+ 0.21	- 1.94	67
Mar.	0.98	-0.65	- 0.53	- 0.83	- 0.87	- 0.55	+ 0.89	0.00	- 2.54	63
Apr.	2.31	-0.17	- 1.94	- 2.10	- 1.29	- 1.93	+ 0.27	- 0.66	- 7.82	51
May	3.28	-0.46	- 1.73	+ 2.99	+ 2.19	- 1.79	+ 4.93	- 2.28	+ 3.85	117
June	3.35	-2.28	+ 1.80	+ 1.75	- 2.64	- 0.67	- 0.62	+ 1.36	- 1.30	95
July	3.32	-1.20	- 2.78	- 3.31	- 2.58	+ 1.62	- 2.24	- 2.28	-12.77	45
Aug.	3.00	-0.27	- 0.22	- 1.02	- 0.85	- 0.18	- 0.53	+ 0.53	- 2.54	86
Sept.	2.29	-0.26	+ 0.19	+ 2.23	- 0.08	- 0.67	- 0.16	- 1.87	- 0.62	96
Oct.	1.51	-1.48	- 0.99	- 0.55	+ 1.15	+ 0.08	- 1.48	- 1.33	- 4.66	57
Nov.	0.86	-0.26	- 0.05	+ 1.37	- 0.80	- 0.40	- 0.50	- 0.69	- 1.33	76
Dec.	0.75	+1.42	- 0.73	- 0.55	- 0.25	- 0.57	- 0.75	- 0.05	- 1.48	72
Total	22.91	-6.65	- 6.85	- 1.04	- 7.01	- 5.05	- 0.80	- 7.06	-34.46	
Accumulated deficits		-6.65	-13.50	-14.54	-21.55	-26.60	-27.40	-34.46		

the extremely dry year of 1939 was over 7 inches. This increased the total for the 7 years to 34.46 inches.

Rainfall data were also compiled for the years 1937, 1938, and 1939 from measurements made at the several stations in western Kansas where quantitative studies were conducted (Fig. 4). At all sta-

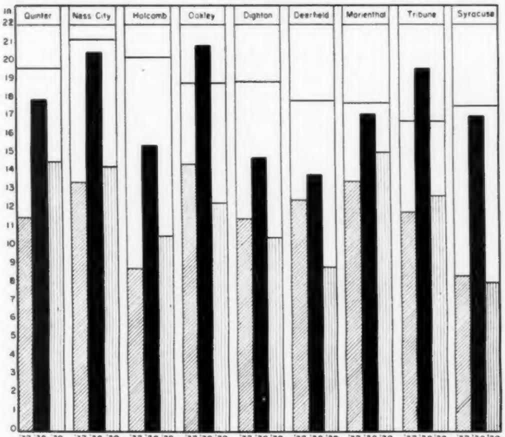

FIG. 4. Mean annual precipitation (horizontal lines) and annual precipitation during 1937, 1938, and 1939, at nine stations in western Kansas.

tions, the precipitation in 1938 was the greatest of the 3 years. In four places, the rainfall for 1937 exceeded that of 1939; in five, the reverse condition prevailed. The normal precipitation, deviation from the normal, the total deficit, and the percent of normal precipitation for these 3 years are given in Table 2. The mean precipitation at Ness City (21.24

TABLE 2. Mean annual precipitation (in inches), deviation from the mean, total deficit, and percent of normal during 1937 to 1939, inclusive, at nine western Kansas stations.

Station	Normal precip-itation	Deviation from normal			Total deficit	Percent of normal rainfall 3 years
		1937	1938	1939		
Quinter	19.56	— 8.08	— 1.57	— 5.02	—14.67	75.0
Ness City	21.24	— 7.86	— 0.88	— 6.97	—15.71	75.3
Holcomb	20.22	—11.35	— 4.78	— 9.77	—25.90	57.3
Oakley	18.83	— 4.49	+ 2.10	— 6.57	— 8.96	84.1
Dighton	18.87	— 7.37	— 4.11	— 8.30	—19.78	65.0
Deerfield	17.89	— 5.20	— 4.15	— 9.06	—18.41	65.7
Marienthal	17.75	— 4.08	— 0.64	— 2.69	— 7.41	86.0
Tribune	16.72	— 4.87	+ 2.93	— 4.05	— 5.99	88.1
Syracuse	17.67	— 9.25	— 0.65	— 9.60	—19.50	63.2

inches) was the greatest at any of the stations where studies were made. It was least at Tribune with 16.72 inches. The precipitation was below normal in every location for each year except 1938, when it was 2.1 and 2.93 inches above the mean at Oakley and Tribune, respectively. The accumulated deficit for the 3 years ranged from 5.99 inches at Tribune to 25.9 at Holcomb. At four of the nine stations, the total for 3 years was actually less than that which would normally be expected in 2 years. The percentage of total normal precipitation for the 3-year period ranged from 57.3 at Holcomb to 88.1 at Tribune.

The deviation from the mean annual precipitation for the entire state, the middle division, the western division, and for Hays is given in Table 3. These data indicate that deficient precipitation did not occur simultaneously over the entire state. For example, the drought did not begin at Hays until 1933, but in the middle division it made its appearance in 1930 and in the western division in 1931.

TABLE 3. Deviation (in inches) from the mean annual precipitation in Kansas, 1927 to 1939, inclusive.

Location	1927	1928	1929	1930	1931	1932	1933
Entire State	+5.63	+6.57	+1.18	0.00	—1.24	—3.54	—4.74
Middle Division	+5.44	+6.45	+2.15	—0.33	—1.79	—3.17	—6.97
Western Division	—0.51	+7.99	—0.13	+3.86	—3.62	—2.39	—1.36
Hays	+4.41	+7.14	+3.77	+2.23	+3.15	+8.75	—6.65

Location	1934	1935	1936	1937	1938	1939
Entire State	—6.77	+1.64	—8.34	—5.66	+0.71	—6.35
Middle Division	—5.76	+1.41	—8.52	—4.07	+2.08	—5.04
Western Division	—8.00	—3.77	—5.21	—6.15	—0.89	—5.91
Hays	—6.85	—1.04	—7.01	—5.05	—0.80	—7.06

TEMPERATURE

The average monthly and mean annual temperatures for the 8-year period immediately preceding the drought (1925 to 1932), those for the 3 best years of the drought (1935, 1937, 1938), and those for the 4 worst years of the drought are shown in Table 4. The average of the years 1925 to 1932 was fairly typical, the mean annual temperature being only .7°F. above normal.

TABLE 4. Average monthly and mean annual temperatures with annual departures from the normal: (A) 1925-1932, (B) for the 3 best years of the drought, and (C) for the 4 worst years of the drought at Hays, Kansas.

Year	January	February	March	April	May	June	July	August	September	October	November	December	Annual	Dep. from normal
A														
Av. '25-'32	27.4	37.0	41.6	53.0	62.5	72.3	79.3	76.9	70.0	55.6	40.7	31.5	54.1	+0.72
B														
1935	34.2	38.2	50.4	52.0	58.4	70.0	83.6	81.0	69.4	54.2	39.2	33.9	55.4	+2.0
1937	18.4	31.2	59.6	53.9	67.2	74.4	82.2	84.1	71.3	56.2	40.0	31.1	54.2	+0.8
1938	33.9	36.0	49.0	53.9	62.0	72.6	82.0	83.7	72.1	64.0	41.4	35.2	57.2	+3.8
Av.	28.8	35.1	46.3	53.2	62.5	72.3	82.0	82.9	70.9	58.1	40.4	3.4	55.5	+2.1
C														
1933	37.8	29.4	46.8	53.5	63.2	80.8	81.5	77.2	74.0	57.4	46.2	38.8	57.2	+3.8
1934	36.2	34.6	42.8	55.7	70.5	80.0	87.1	82.5	65.0	61.8	46.4	31.8	57.8	+4.4
1936	26.9	20.8	46.8	53.0	66.8	76.4	85.6	84.2	72.0	54.0	42.0	36.4	55.4	+2.0
1939	22.8	28.7	43.2	53.7	68.0	75.4	84.7	78.0	75.2	59.7	43.0	37.2	55.8	+2.4
Av.	30.9	28.3	44.9	53.9	67.2	78.1	84.7	80.4	71.5	58.2	44.4	36.0	56.5	+3.1

During the 3 years 1935, 1937, and 1938, the mean annual temperature was 2.1° above normal, and in 1938, the year of greatest rainfall, it was 3.8° above normal. The average for the 4 worst years of the drought (1933, 1934, 1936, 1939) was 3.1° above normal. The greatest departure from normal was in 1934 when the mean annual temperature averaged 4.4° above.

The monthly average of maximum daily temperatures for the growing season (April to September) has a profound effect upon the vegetation. At no time during the growing seasons of 1925 to 1932, inclusive, did the average daily maximum for the month reach 100°F. (Table 5). The average for July during this 8-year period was 93.1°. It varied from 96.7° in July, 1930, to 88.7° in 1928. The average maximum daily temperatures for June and August were 7.9° and 2.7°, respectively, below that of July. These temperatures are in direct contrast with those of the drought years when the temperature was not only much higher but high temperatures also of much greater duration. For example, the average daily maximum for July, 1935, 1937, and 1938, was 4.7° above the fairly normal period of 1925 to 1932. In making the same comparison for August, a difference of 7.5° was found. The temperature during the 4 driest years of the drought was even higher and of greater duration. The average maximums for June, July, and August were 93.2°, 100.6°, and 94.8°, respectively, or 8.0°, 7.5°, and 4.4° higher than the fairly normal period of 1925 to 1932.

The average maximum temperatures for the three periods (predrought period, 3 best years of drought, and 4 worst years of drought) were nearly the same in April and again in September. This is likewise true for the mean daily temperatures (Fig. 5). In

TABLE 5. Monthly average of maximum daily temperatures at Hays, Kansas: (A) for 6 summer months of 1925 to 1932, (B) for 1935, 1937, 1938, and (C) for 1933, 1934, 1936, 1939.

Year	April	May	June	July	August	Sept.
A						
1925......	70.9	75.5	92.6	93.1	89.2	85.3
1926......	62.7	78.6	88.5	94.5	95.9	81.3
1927......	68.5	78.1	82.0	90.1	82.2	82.1
1928......	65.2	76.9	75.6	88.7	89.0	83.7
1929......	69.6	71.8	83.9	91.7	91.7	80.1
1930......	72.3	74.5	84.0	96.7	93.5	84.3
1931......	64.8	71.5	91.0	93.7	90.1	93.7
1932......	70.7	79.4	84.1	96.4	91.7	80.7
Average...	68.0	75.9	85.2	93.1	90.4	83.9
B						
1935......	65.3	68.1	81.2	99.1	95.8	83.8
1937......	70.0	81.3	87.9	96.9	99.0	85.5
1938......	66.1	73.8	85.2	97.6	99.0	87.2
Average...	67.1	74.4	84.7	97.8	97.9	85.5
C						
1933......	66.3	77.3	97.2	96.3	90.4	89.0
1934......	71.6	85.5	94.7	103.6	97.1	78.8
1936......	69.6	77.8	91.6	101.4	100.3	84.0
1939......	67.6	84.2	89.3	101.1	91.7	91.5
Average...	68.7	81.2	93.2	100.6	94.8	85.8

general, differences increased from April, reached a maximum in July, and gradually decreased until they were negligible by the end of August.

WIND MOVEMENT

Total miles of wind movement for each month of the growing season for the drought years are given in Table 6.[3] April had the greatest average wind

TABLE 6. Total miles of wind movement per month at Hays, Kansas, during the growing seasons of 1933 to 1939, inclusive. Also, the average for the 32-year period (1908 to 1939) and the drought period (1933 to 1939).

Year	April	May	June	July	Aug.	Sept.	Total for growing season
1933........	6,931	6,360	5,976	5,040	4,920	5,592	34,819
1934........	6,550	7,488	7,056	7,416	6,192	7,080	41,782
1935........	9,657	7,608	5,832	6,048	6,120	5,880	41,145
1936........	6,876	5,712	4,824	5,760	4,440	6,216	33,828
1937........	7,809	6,912	6,212	5,424	8,256	5,328	39,941
1938........	8,505	5,664	4,944	5,016	6,648	4,680	35,457
1939........	7,528	7,104	7,080	6,268	5,760	6,960	40,700
Average.....	7,693	6,692	5,989	5,853	6,048	5,961	38,239
1908 to 1939.	7,452	6,540	5,746	5,237	5,218	5,978	36,171

velocity for the drought period. The total number of miles of wind movement per month for the growing season was highest for April during 5 of the 7 years. The average for the 7-year period (7,693 miles) was approximately 1,000 miles greater than for May and over 1,600 miles greater than for August. In 1935, April had a total wind movement of 9,657 miles, which was over 1,100 miles greater than April, 1938, and nearly 2,000 miles greater than the monthly average for the drought period.

[3] Data on wind movement and evaporation were obtained from measurements made at Hays, Kansas, by the Division of Dry Land Agriculture, Bureau of Plant Industry, U. S. Department of Agriculture.

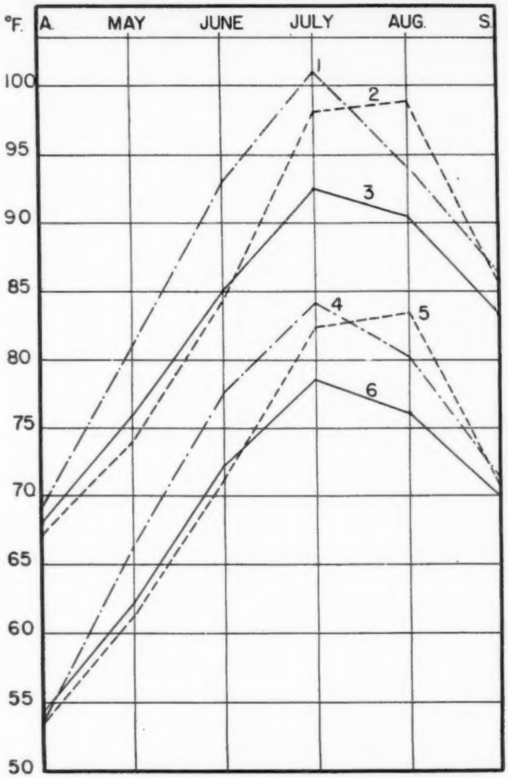

FIG. 5. Graphs showing average daily maximum temperature: 1, of 4 worst drought years (1933, 1934, 1936, and 1939); 2, of 3 best drought years (1935, 1937, and 1938); and 3, of predrought period (1925 to 1932). Mean daily temperatures: 4, of 4 worst drought years; 5, of 3 best drought years; and 6, of predrought period.

The average total wind movement per month for the drought period was greater than the normal (1908 to 1939) for every month of the growing season except September, which was only slightly below normal. The total wind movement for the growing season of 1934 was highest, being 41,782 miles. That of 1935 and 1939 was only slightly less—41,145 and 40,700 miles, respectively. Wind movement for the growing season of 1935 totaled high because of the very strong winds of April and early May. The remaining 2 years of most severe drought (1933 and 1936) had less wind movement—34,819 and 33,828 miles, respectively. There were three seasons (1933, 1936, and 1938) for which the total wind movement for the season was below normal. During the remaining four seasons wind movement ranged from 3,770 miles (in 1937) to 5,611 miles (in 1934) above normal.

DUST STORMS

The combined effects of cultivation, overgrazing, and drought created a condition in the surface soil which was extremely conducive to the blowing of dust by the wind. Deficient rainfall in the middle and western portion of the state of Kansas began in 1931 (Table 3). As the soil became drier and more barren, cultivation was more effective in pulverizing the surface soil to the extent that it could be easily lifted by the wind. Dust storms in western Kansas were frequent but not severe during 1932. In 1933 there were many local dust storms and several were of wide extent and especially severe on April 13, 19, and 29. Lights were necessary in the middle of the afternoon, and such darkness prevailed that chickens went to roost soon after midday.

The season of 1934 was not considered a dusty one, even though it was extremely dry. Dust storms were more frequent and widespread in April, however, than they had been in any other month in the history of the state.

The blowing of dust reached a climax in March and April of 1935. The extremely high wind velocity during these two months was all that was necessary to initiate the black blizzards in the vast areas covered with dry, pulverized soil. Even as early as February 21 and 24, dust storms were unusually severe. They occurred on approximately half of the days after March 15; in fact, on some occasions, the air was filled with dust for a period of several days at a time. Often a dust storm approaching from a distance had much the appearance of an extremely dark rain cloud, being driven by a wind of high velocity (Fig. 6).

Photo by Conard

FIG. 6. Dust storms at Hugoton in southwestern Kansas, typical of the black blizzards of the great drought.

Visibility in the areas covered by these "dusters" was often reduced to only a few feet or even to zero. It was then necessary to follow the pavement curb and count the streets to find one's way home. Dust penetrated every crevice in the houses. As much as a quarter of an inch of dust accumulated over the floors and furniture. The dust storm of late afternoon and night of March 15 and 16 was reported to have been the most severe and most damaging ever known in northwestern and north-central Kansas. Traffic on the highways was abandoned; trains were delayed; and, on many occasions, people were obliged to cover their faces with dampened handkerchiefs in order to breathe.

Much of the dust that was moved about was not actually suspended in the air but carried along the surface of the soil. The few growing plants that remained were often cut away as if they had been subjected to the action of a sand blast. In sections of the dust bowl, fence posts were not infrequently worn away so that only a small portion in the center remained. Enormous, tortuous drifts of soil, often as high as 30 inches, were deposited over the prairies, especially where vegetation such as yucca, sagebrush, or cactus caused the accumulation of soil. Vast areas of vegetation were smothered by the drifts of loose soil (Fig. 7).

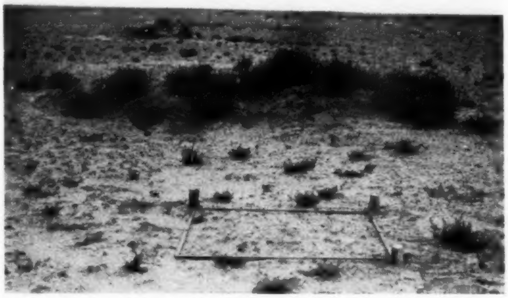

FIG. 7. Large drifts of dust, frequently 30 inches in height, were distributed over many of the grasslands of western Kansas. These drifts were later partially covered by Russian thistles and other weeds. Sometimes, as on this range, they were inhabited by pack rats.

Usually much of the fine silt was suspended in the air and often carried great distances and deposited where no actual blowing of the soil had occurred.[4] Extensive grasslands that lay far from cultivated fields were commonly covered by a layer of this fine silt to a depth of ½ inch to over 1 inch. "Dusting" of this nature was continued late into April, 1935, and, according to records, the air was filled with dust 15 to 25 days of the month. The rains of May and June ameliorated the condition by settling the soil and promoting the germination of weed seeds. Weeds soon covered much of the soil with a green blanket. Stabilization was temporary and on many occasions dust storms of a local nature occurred in the dust bowl. While this catastrophe was greatest and most intensive during 1935, it by no means constituted the only period when dust storms occurred.

During 1936, there was considerable soil movement in some sections of the western portion of the state.

[4] During the great dust storm of March 20 to 22, 1935, the Department of Geology of the University of Wichita, at Wichita, Kansas, "weighed" the atmosphere. They estimated that 5,000,000 tons of dust were suspended over the area of 30 square miles occupied by the city in a layer of atmosphere one mile thick. However, the dust extended upward to a height of more than 12,000 feet and the source area of the dust was 250 miles westward (Lugn, 1939).

Much of the dust-blowing in cultivated fields subsequent to 1936 was prevented by improved cultural practices. On numerous occasions the writers have witnessed severe dust storms where the soil was actually lifted from prairies that were previously denuded by deposits of dust from cultivated fields. This type of dusting is difficult to control since cultivation, in many instances, is either undesirable or impossible (Joel, 1937).

EVAPORATION

The average monthly evaporation from a free water surface during the growing season for a period of 32 years (1907 to 1938) gradually increased from 5.9 inches in April to 10.5 in July, after which it decreased to 7.4 in September (Table 7). A total of 48.5 inches was recorded for the entire growing season. The greatest seasonal evaporation during the drought period was 66.4 inches in 1934. This was followed by 58.9 inches in 1936 and 60.9 inches in 1939. The other extremely dry year, 1933, had a seasonal evaporation of 56.5 inches.

TABLE 7. Average monthly evaporation in inches from a free water surface (1907 to 1938), and average deviation from the mean during the growing seasons of seven years of drought at Hays, Kansas.

Year	April	May	June	July	Aug.	Sept.	Total
Av. 1907 to 1938 inclusive (32 yrs.)	5.9	6.8	8.4	10.5	9.6	7.4	48.5
1933	6.9	7.0	12.9	12.4	8.9	8.4	56.5
1934	7.0	10.8	12.6	16.3	13.1	6.6	66.4
1935	7.3	5.5	6.9	13.1	11.3	7.5	51.6
1936	7.3	6.8	10.1	14.6	12.1	8.0	58.9
1937	6.8	8.4	9.9	11.5	11.3	7.9	55.8
1938	5.2	4.7	7.7	11.2	12.4	7.8	49.0
1939	5.9	9.5	11.3	13.6	9.8	10.8	60.9
Deviation from mean	+ .7	+ .7	+1.8	+2.7	+1.7	+ .7	+8.5
Av. 1933, 1934, 1936, 1939	6.8	8.5	11.7	14.2	10.9	8.4	60.7
Av. 1935, 1937. 1938	6.4	6.2	8.2	11.9	11.8	7.7	52.1
Av. for 1933 to 1939	6.6	7.5	10.2	13.2	11.3	8.1	57.0

The greatest average monthly deviation from the mean occurred in July and was +2.7 inches. It was 1.8 inches above normal in June, 1.7 inches in August, and 0.7 inch in each of the 3 remaining months, April, May, and September. Evaporation during the drought years was 8.5 inches above normal for the growing season. The average monthly evaporation for the 4 driest years was highest in July, being 14.2 inches. April had the lowest average evaporation which was 6.8 inches above normal. The average rate of evaporation for the 3 best years of the drought (1935, 1937, and 1938) was 6.4 inches during April, and 6.2 inches in May, after which it rose rapidly and reached its maximum of 11.9 inches in July.

WATER CONTENT OF SOIL

The amount of moisture in the soil is especially important in the Great Plains region, since it is nearly always the limiting factor in plant production. Available soil moisture was determined in the first and second 6-inch depths and in 12-inch soil cores taken with a Briggs' geotome to a depth of 5 feet. Except for 1936, samples were obtained at weekly intervals from the third week of May to the second week of September throughout the entire period of drought. Other samplings were made at irregular intervals in early spring and in late fall. Total water content of soil minus the hygroscopic coefficient (which was determined for each soil depth) is designated as water available for growth. In this manner, the water content of soil upon which vegetation existed during the drought period was definitely ascertained (Fig. 8).

As a result of the wet year of 1932, there was sufficient moisture stored in the soil of the short-grass type of grassland to insure rapid growth in the early spring of 1933. Available water early in 1933 extended throughout the depth to which determinations were made. The top 12 inches contained more than 10 percent available water, and from the 12-inch depth to 3 feet, there was only slightly less. From the 3-foot level to 5 feet, nearly 5 percent of water was present.

As the season progressed, the quantity of available moisture rapidly diminished, especially in the upper portion of the soil. By the first week in June, no moisture was available in the first 12 inches; less than 5 percent was available in the second and fifth foot, and less than 2 percent in the third and fourth foot. By the second week in June, no moisture was available to 3 feet and less than 5 percent below that depth. This condition continued until the first week of July, with the exception of less than 2 percent in the first 6 inches during the third week in June, caused by local showers. During the second, third, and fourth weeks of July, from 8.3 percent to less than 2 percent was available in the upper 12 inches. During the first two weeks of August no moisture was available to a depth of 3 feet. Intermittent showers during the last half of August and the first half of September resulted in as much as 7.3 percent available moisture in the upper 6 inches. The amount of water between the 3- and 5-foot levels remained rather constant throughout the season, but at no time was the amount above 5 percent.

March and April of 1934 were unusually dry and by the third week of May there was less than 2 percent available moisture in the upper 6 inches and none below this depth to at least 5 feet. This condition remained constant until the third week of June, when approximately 5 inches of rainfall increased the amount of available moisture to 18.5 percent in the upper 6 inches and 12.8 percent in the second 6 inches. The increase in moisture in the second foot was almost negligible. This moisture was rapidly dissipated through evaporation and transpiration and lasted but 3 weeks. From the second

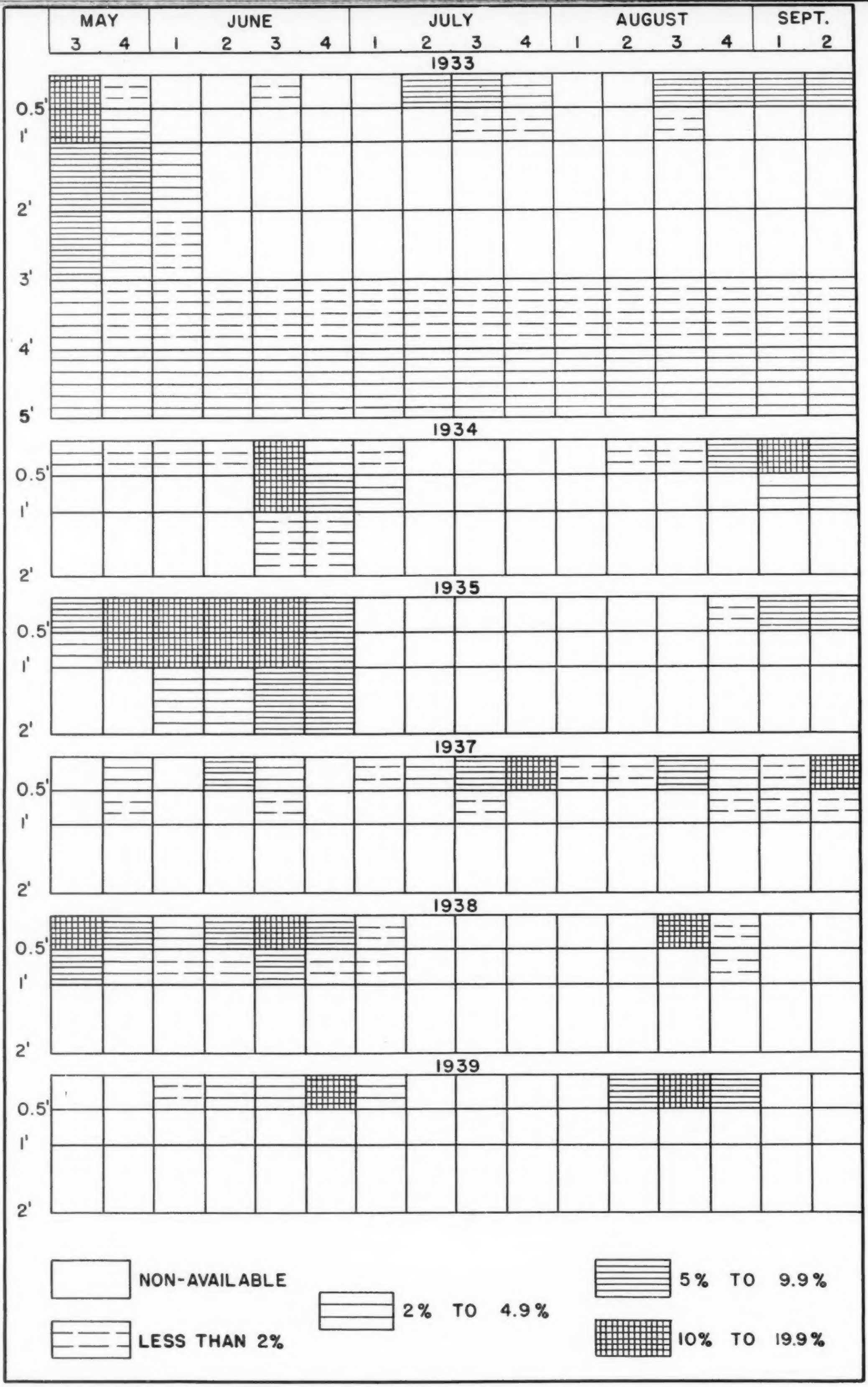

FIG. 8. Available soil moisture to a depth of 5 feet in short-grass (Buchloe-Bouteloua) habitat, Hays, Kansas. No moisture was available below 2 feet during 1934 to 1939, inclusive, hence the 3- to 5-foot levels are not shown.

week of July until the fourth week of August, there was no moisture available at any depth except in the upper 6 inches, where the amount was less than 2 percent. The rains during the latter part of August and early September brought the total available moisture to slightly more than 10 percent in the upper 6 inches. Less than 5 percent was available for plant growth in the second 6 inches and none below this depth. A small amount of available moisture in the upper 12 inches was present throughout the month of September, which gave the scanty stand of living vegetation an opportunity to produce some fall growth.

The early spring of 1935 was extremely dry and windy. Soil moisture determinations made during March and April showed that practically no available moisture was present during this time. The rains during the latter part of May and nearly all of June stored available moisture to a maximum depth of 24 inches. The greatest amount available at any one time was 14.7 percent in the upper 6 inches during the last week of May. This condition was maintained for 4 weeks, after which the available moisture rapidly diminished and for a period of 7 weeks during July and August there was none. Rainfall during late September, 1935, increased the amount of available moisture to 20 percent in the upper 6 inches.

The number of moisture determinations made during 1936 was insufficient to make it possible to include them in chart form. The amount of available moisture, however, was extremely low and where present was limited to the upper 6 inches.

There was no available moisture at any depth except the upper 12 inches in 1937. During 3 of the 16 weeks when moisture determinations were made, no available water was found at any depth. The amount present during the 13 weeks varied from 1.2 percent for the first week of July to 13.6 percent for the fourth week of the same month. The amount for the third week of August and the second week of September was 8.0 and 12.9 percent, respectively, in the upper 6 inches. Less than 2 percent was available in the 6- to 12-inch level during 6 of the 16 weeks and none was available during the remaining 10 weeks.

The nearly normal rainfall of 1938 failed to store available moisture in the soil to a depth greater than 12 inches. During the third week of May, 12.9 percent available moisture was found in the upper 6 inches and 5.8 percent in the second 6 inches. This supply gradually diminished until the showers during the third week of June restored the amount to 12.4 in the upper 6 inches and 5.7 in the second 6 inches. By the second week of July, all available moisture had been used by the growing vegetation. From this time until the third week of August, a period of 5 weeks, no available moisture was present. The rains during the third week of August, however, brought the total amount available to plant use up to 12.9 percent. Since this was all in the surface 6 inches, it was quickly lost through evaporation and transpiration.

There was never any available soil moisture below 6 inches during the extremely dry season of 1939. The amount in the upper 6 inches was never greater than 10 percent except during the fourth week of June and the third week of August. Less than 5 percent was present during 3 weeks of June and less than 10 percent during the second and fourth weeks of August. It is significant that even with showers as great as 1.5 inches, such as the one received on June 14, comparatively little water was stored in the soil. The explanation of this doubtless lies in the fact that much of a dashing rain of this amount, because of the relatively impervious soil and scarcity of vegetation, is lost to the location where it falls and becomes a flood hazard in the valleys below. Soil moisture determinations made later in the autumn of 1939 revealed that no moisture was available at any depth to 5 feet after August.

COACTIONS

Depletion of the ranges during drought has greatly intensified the grazing on practically all pasture land. The carrying capacity of large areas has been greatly reduced. Where formerly 1 animal unit required a grazing range of 10 to 12 acres, 30 to 50 acres are now needed. The farmers, in many instances, found it difficult to reduce the number of livestock to a conservative stocking rate; consequently, most of the grassland in the Great Plains region has been seriously overgrazed. Furthermore, decreased forage has caused a reduction in the quantity and quality of meat produced by the livestock. During recent years it has been impossible to carry livestock through the summer without supplemental feed.

Grasshoppers have further added to the deterioration of the range. On numerous occasions, as many as 8 to 12 per square foot have been found feeding upon the weeds and grasses in the native pastures. Preliminary investigations indicate that, during periods of extreme drought, a large percentage of the vegetation is consumed by the hungry grasshoppers.

TYPES OF VEGETATION

There are three types of vegetation, with varying degrees of intermixtures, that are common in the mixed prairie of west-central Kansas, especially in those regions where there is an outcrop of limestone, such as Smoky Hill Chalk, Fort Hays Limestone, and Benton Limestone (Fig. 9).

The little-bluestem *(Andropogon scoparius)* type is most extensive, occupying about 60 percent of the area. This type is commonly found on the hillsides and in shallow ravines. Under favorable environmental conditions, it extends over the brows of the hills and far into the short-grass areas if the slope is gentle. If the slope is steep, however, the transition from one type to the other is rather abrupt.

FIG. 9. Range land near Hays, Kansas, showing the Buchloe-Bouteloua type occupying the immediate foreground and distant background (light color), and the *Andropogon scoparius* type (dark) occurring in the ravine and on the slope. Photo, 1934 near Hays, Kansas.

Photo by L. D. Wooster

FIG. 10. *Andropogon scoparius* type (dark areas) and Buchloe-Bouteloua type (light areas) occupied the gentle slopes in 1930 before the drought. Photo in 1930 near Hays, Kansas.

FIG. 11. View of the same general area as shown in Fig. 10 as it appeared in May of 1939, after 7 years of drought. A sparse cover of short grasses has replaced the little bluestem. Hays, Kansas.

The short-grass (Buchloe-Bouteloua) type constitutes approximately 30 percent of the prairies and is found widely distributed over the nearly level uplands. Smaller areas and strips also occur on gentle slopes and at the bases of hills, especially on south-facing slopes (Albertson, 1937). Farther to the southwest, where much of the land is comparatively level, the short-grass type predominates, and in many areas, due to overgrazing, the mid grasses have been almost completely replaced by the short grasses.

An ecotone or transition zone between the little-bluestem and short-grass types is composed of two layers of grasses, scattered bunches of little bluestem, wire grass (*Aristida* spp.), and side-oats grama (*Bouteloua curtipendula*) forming the upper layer and the short grasses the lower one.

The big-bluestem (*Andropogon furcatus*) type is of much less importance and is generally limited to the larger ravines and protected slopes (Clements, 1936).

CHANGES IN VEGETATION

Vegetation that has become adapted to the variable climatic conditions in the Great Plains region has been compelled to undergo a state of dormancy or semidormancy several times during the growing season. During the period of 7 years of drought, the vegetation has frequently been subjected to such severe desiccation that for days at a time much wilting occurred. Often buffalo grass (*Buchloe dactyloides*), blue grama grass (*Bouteloua gracilis*), and even other species became so dry that when trodden upon they crackled underfoot (Shantz, 1923).

Short grasses growing on the tablelands were the first to manifest effects of drought. The ordinary straw color accompanying dormancy usually appeared several times during the season, but in 1934 and 1939 much of the vegetation became bluish-gray, a color indicative of death. Many mesic plants disappeared completely and were replaced by others less susceptible to drought. Even the more xeric were often very much reduced in numbers (Figs. 10 and 11) (Albertson, 1938; 1939).

Animal life was materially affected by drought and dust. This was especially true of the ground-dwelling species of mammals and birds. The number of jack rabbits, prairie chickens, quails, and horned larks, for example, was reported to have been greatly reduced in some areas (Wooster, 1935; 1939). The destructive effect of drought on the vegetation upon which they fed has been traced annually by means of scores of permanent quadrats.

CHANGES IN ANDROPOGON SCOPARIUS TYPE

Studies in the *Andropogon scoparius* type were begun in 1932 when stock was excluded from several representative areas, which had been moderately grazed for many years. Numerous meter quadrats were staked out and permanently marked for future study. These quadrats were charted in the fall of 1932 and each subsequent autumn except 1936.

UNGRAZED CLOSED TYPE OF ANDROPOGON SCOPARIUS

The percentage of basal cover afforded by each species for each year in this type is shown in Table 8.

TABLE 8. Change in percentage of basal cover in 15 meter quadrats in an ungrazed, closed type of *Andropogon scoparius* at Hays, Kansas, from 1932 to 1939. The data are from two groups of quadrats but the response of the vegetation is similar in both.*

Species	1932	1934	1935	1936	1937	1938	1939
Andropogon scoparius	49.6	37.2	9.6	3.5	1.4	.9	.6
Andropogon furcatus	10.7	5.5	8.5	4.6	5.3	3.2	2.2
Bouteloua curtipendula	.....	3.1	6.1	6.2	12.1	17.7	17.6
Bouteloua gracilis	.....	.7	2.1	1.8	5.6	7.8	8.8
Bouteloua hirsuta	.....	.4	.3	.....	.3	.3	.3
Sporobolus pilosus	.....	.....	.1	.0	.3	.4	.4
Buchloe dactyloides	.....	.....	.....	.....	.....	.1	.3
Total	60.3	46.9	26.7	16.1	25.0	30.4	30.2
Andropogon scoparius	.....	.....	22.1	8.3	3.3	3.4	3.5
Bouteloua curtipendula	.....	.....	3.9	4.4	10.4	11.5	14.1
Andropogon furcatus	.....	.....	5.8	2.9	1.2	.4	.8
Bouteloua gracilis	.....	.....	.3	.4	1.3	1.5	3.3
Bouteloua hirsuta	.....	.....	.1	.....	.0	.1	.2
Sporobolus pilosus	.....	.....	.....	.....	.....	.5	.....
Total	.....	.....	32.2	16.0	16.2	17.4	21.9

*Forbs are not included in this paper because of limitations of space; they will be treated separately. The presence or absence of ruderals at the time of quadratting was largely determined by variations in seasonal conditions. Native forbs have been greatly depleted in numbers or have disappeared.

Little bluestem constituted the major portion of the vegetation when these studies were initiated (Fig. 12). Its associate, big bluestem, formed approximately one sixth of the total plant cover. The basal cover averaged about 60 percent. Less than this amount was frequently found because of excessive debris resulting from dead vegetation accumulated through previous years. Slight increases occurred where grazing was heavy enough to prevent this accumulation but not so intense as actually to damage the bluestems.

Photo by L. D. Wooster

FIG. 12. Typical *Andropogon scoparius* type of grassland at Hays, Kansas.

The average basal cover of nine quadrats was gradually reduced from 60.3 percent in 1932 to a minimum of 16.1 percent in 1936. The somewhat better years of 1937 and 1938 brought some improvement. The basal cover was increased to 25 percent in 1937, to 30.4 in 1938, and to 30.2 percent in 1939. It is evident that the accumulated benefits derived from the nearly normal year of 1938 carried over into 1939, when the rainfall was the least of any year during the entire period of drought. The shifting of the various plant species is shown in Figure 13.

The characteristic appearance of the ungrazed little-bluestem type which prevailed during the period of favorable growing conditions was gradually but definitely lost soon after the onslaught of the drought, which began in 1933. The dried tops of little bluestem of 1932 showed clearly that under favorable conditions this grass reaches a height of about 2 feet. Growth during 1933 was irregular and seldom approached normal except in certain favored places where there was more available moisture than

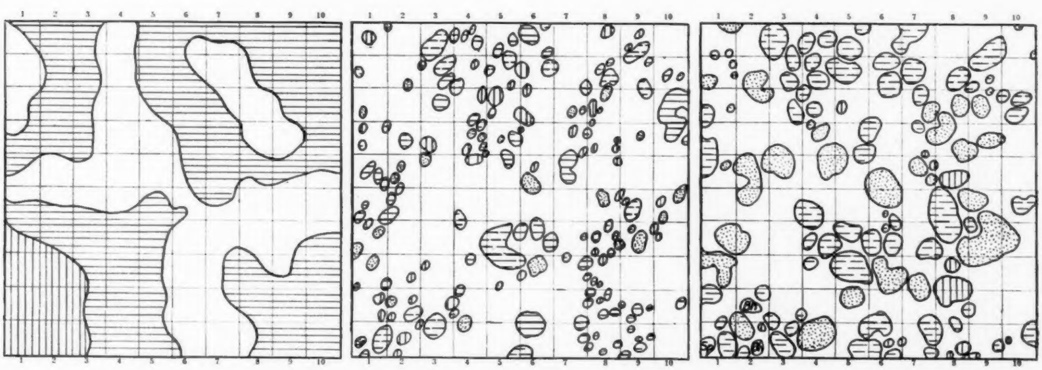

FIG. 13. Quadrat in an ungrazed, closed type of *Andropogon scoparius* charted in the fall of 1932 (left), 1936 (center), and 1939 (right). In 1932 *Andropogon scoparius* (horizontal hatch) had a basal cover of 67.5 percent. The cover of *Andropogon furcatus* (vertical hatch) was 7.7 percent. The bluestems were replaced primarily by *Bouteloua curtipendula* (broken horizontal hatch) and *Bouteloua gracilis* (small dots). Hairy grama (*Bouteloua hirsuta*) (Bh), and hairy dropseed (*Sporobolus pilosus*) (Sp) were never abundant. The open space is bare ground. The large amount of open space (not hatched) in 1932 (24.8 percent) was due to previous excessive debris. That in 1936 (85.5 percent) and 1939 (68.2 percent) resulted in the main from drought.

was found elsewhere. By the middle of June, 1933, this chief dominant had grown but little, and the folded leaves were a definite sign of drought. The more deeply rooted big bluestem, however, was from 9 inches to 15 inches tall and apparently little affected by drought.

By the first of July, there was no available moisture[5] in the upper 24 inches and many of the grasses were showing more definite signs of soil moisture deficiency. Only the deeply rooted forbs such as lead plant *(Amorpha canescens)* and few-flowered psoralea *(Psoralea tenuiflora)* were fresh and green.

The early spring of 1934 was unusually dry and renewal of growth was much delayed. The rains of June, however, did much to revive the drought-stricken vegetation, and growth continued until early in July when, because of extreme heat (112°F.), low relative humidity (9 percent), and deficient soil moisture, much of the vegetation in this habitat was forced into dormancy. This condition continued until the slightly above normal precipitation of September stimulated some fall growth. It was observed during the fall of 1934 that many of the young native plants, both grasses and forbs, and the older bunches of grass, had suffered severely from drought. The basal cover had decreased from 60.3 percent to about 47 percent.

The heavy rains of late May and early June of 1935 washed away much of the dust that had accumulated on the vegetation in this habitat. Vegetation that remained after 2 years of drought and a severe dusting renewed growth with much vigor during June when the surface soil was continuously moist. The supply of available soil moisture, however, was soon exhausted and by the middle of July the little bluestem, now 12 inches high, began to wilt and was soon forced into dormancy. The effects of drought became much more intense on south-facing slopes than on those facing northward. Furthermore, the xeric strips of short grasses commonly found on the lower slopes, with bluestems both above and below (Albertson, 1937), became widened by short grasses invading the vegetation both above and below their usual habitat.[6]

The accumulated effects of 1933, 1934, and 1935, added to the extremely dry year of 1936, was nothing less than a catastrophe to the bulk of the living plants. The rains of May (1936) were sufficient to support growth for only a few weeks, after which the extremely dry weather of June and July reduced the basal cover to 16.1 percent. This was scarcely more than one fourth the original amount (Fig. 14).

Even though the rainfall for the year 1937 was somewhat greater than for three of the four preceding ones, the amount received during the growing season was below normal in every month except July. It was the rainfall of July and August that caused

FIG. 14. *Andropogon scoparius* on a gentle slope on a range near Hays, Kansas, in 1936. The open sod in the foreground was caused by 4 years of drought. The short grasses (light) have replaced much of the little bluestem.

late summer growth, which in turn resulted in a slight increase in cover over that of the previous year.

The rains of April and May of 1938 were conducive to both the germination of seed and the rapid growth of the living portion of native plant cover. Remnants of little bluestem were found only rarely where the continued drought had failed completely to destroy them. Big bluestem was also found to contain small live fragments scattered sparsely through the area which it originally occupied.

Myriads of seedlings appeared in the open spaces between the bunches of living grasses. On numerous occasions, as many as 50 to 75 per square foot, mostly those of side-oats grama and hairy grama, were found. These seedlings were of greatest abundance near the parent plants where the soil surface was protected from drying during the period of seed germination. The drought of July and early August greatly reduced the number of live seedlings. It was not uncommon to find numerous seedlings with 3 to 5 brown leaves that had withered and fallen. Examination revealed that the roots had penetrated less than 12 inches into the soil, which now had no available moisture. It was estimated that 90 percent of the seedlings perished during this dry period.

The mature vegetation fared considerably better than did the seedlings. The clay pockets in the rock crevices between the 2- and 8-foot depth were well supplied with moisture by the spring rains. This supply was sufficient to support rather continuous growth throughout the season. By August most of the grasses were fruiting. The effects of the drought were manifest, however, in the small percentage of caryopses produced in relation to the number of florets. The adverse growing conditions were most intense in 1938 during the time when many of the grasses were in full blossom. This condition was doubtless instrumental in reducing the yield of caryopses to almost zero in many locations. It is significant that the best yields of seed were obtained in buffalo wallows, on north-facing slopes, and in similarly better-watered places.

The year of 1939 was the driest of all during this drought period. The rains of June and August were

[5] Soil moisture determinations were regularly made in the little-bluestem and big-bluestem habitats during 1933 and intermittently thereafter. These data, however, are not included in chart form.

[6] The narrow strips of short grasses on the lower slopes are usually underlaid with a highly impervious clay soil which has resulted from disintegrated shale.

slightly above normal. But being separated by the hot, dry month of July, the rainfall of June, in particular, was relatively ineffective. Showers in August, however, aided materially the struggling grasses in producing flower stalks and, in a few cases, an extremely low percentage of caryopses. The reserve of soil moisture carried over from 1938 plus the small amount received during the growing season of 1939 was sufficient to maintain the basal cover of approximately 30 percent produced during the previous year (Fig. 15).

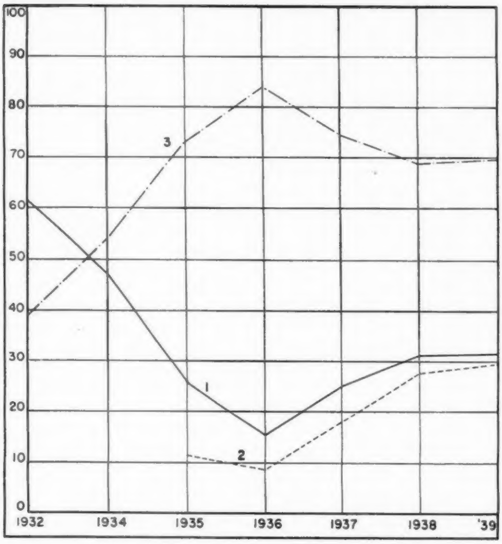

FIG. 15. Graphs showing the percentage of basal cover during the several years of drought in (1) ungrazed and (2) overgrazed *Andropogon scoparius* type. The percentage of bare ground is shown by graph 3.

A decrease in the basal cover and a corresponding increase in bare ground were not the only things of interest that occurred during these 7 years. The direction of movement of all vegetation was toward locations where environmental conditions, especially soil moisture, were more conducive to plant growth.

Little bluestem, which furnished the major portion of vegetation at the beginning of the drought, rapidly decreased to practically nil by 1939. Large areas of comparatively level pastures were often found to be completely devoid of this species. Sometimes a few dwarfed, weak stems grew from the periphery of some of the nearly dead bunches.

Big bluestem, though it suffered severe losses, survived better than its associate. This was attributed, in part, to the greater depth to which its roots penetrated but also to the considerable quantities of reserve food in the crowns and rhizomes which occupied a large portion of the soil. This stored food was doubtless of great value in maintaining life at low ebb during periods of most severe drought. The average basal cover of this species was 10.7 percent in 1932. Loss was continuous but irregular throughout

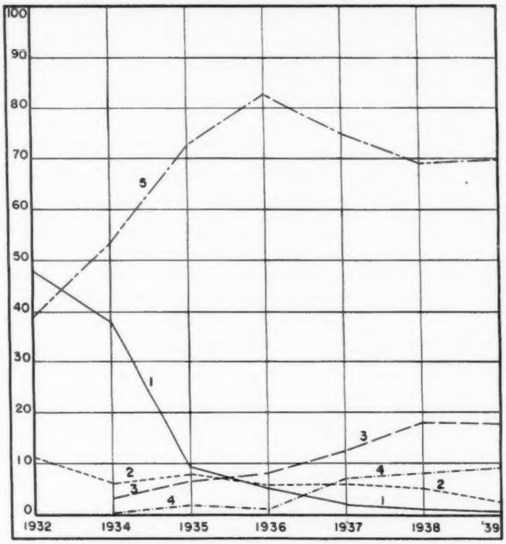

FIG. 16. Percentage of basal cover of various grasses in the ungrazed *Andropogon scoparius* type. (1) Little bluestem and (2) big bluestem were the only grasses present in 1932. (3) Side-oats grama and (4) blue grama were first found in 1934. The percentage of bare ground (5) reached its maximum in 1936.

the drought period, and in 1939, only an average cover of 2.2 percent remained.

Side-oats grama, being more xeric than the bluestems, spread considerably and occupied a portion of the soil bared by the death of the bluestems (Table 8 and Fig. 16). This grass first appeared in the quadrats in the fall of 1934 in an abundance of only 3.1 percent. It is significant that thereafter the increase was continuous, and by 1938 this species constituted over half the vegetation (Fig. 17). Observations showed that much of the increase accrued from new plants produced from the numerous rhizomes 1 to 5 inches long which radiated in all directions from the margins of the parent plants. Such young shoots survived drought much better than did seedlings. In

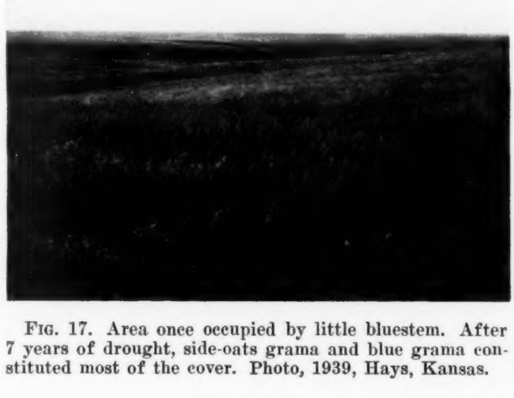

FIG. 17. Area once occupied by little bluestem. After 7 years of drought, side-oats grama and blue grama constituted most of the cover. Photo, 1939, Hays, Kansas.

fact, it was found that when death occurred in this species, it was usually the center of large clumps that died rather than the younger plants produced from rhizomes.

Blue grama, which also made its first appearance in 1934, spread downward from the Buchloe-Bouteloua disclimax above. Increase in number of plants was accomplished by the development of seedlings but increase in size results from addition of new tillers at the periphery of the bunches. This species occupied less than 1 percent of the area in 1934. It scarcely showed consistent gains until 1937. It had increased to 2.1 percent in 1935 but decreased to 1.8 percent in 1936. Thereafter small gains were gradual but constant. In 1939 the average basal cover was 8.8 percent.

UNGRAZED OPEN TYPE OF ANDROPOGON SCOPARIUS

The most common vegetation on the brows of the hills, where the underlying limestone is at or near the surface, is of the open-bunch type. It was not unusual to find only a few scattered tufts of little bluestem, hairy grama, and hairy dropseed, with a considerable sprinkling of dwarfed forbs, in the open spaces between the bunches. Due to the sparseness of vegetation and the frequent mulch of partially disintegrated fragments of limestone, it seems probable that depletion of soil moisture through transpiration and evaporation from the soil surface occurs more slowly than from the more densely populated, deeper soil.

In 1932 the average basal cover of a group of several representative quadrats was 25.5 percent (Table 9). The loss of the dominant was negligible

TABLE 9. Change in percentage of basal cover in an ungrazed open type of *Andropogon scoparius* at Hays, Kansas.

Species	1932	1934	1935	1936	1937	1938	1939
Andropogon scoparius	25.3	23.4	11.4	7.3	4.3	6.4	5.6
Bouteloua curtipendula	.....	2.3	1.1	3.9	8.1	10.7	11.1
Bouteloua hirsuta	.2	.9	.2	.5	.7	1.3	1.2
Andropogon furcatus	.....	.3	.4	.....	.3	.3	.....
Sporobolus pilosus	.....	.....	.....	.1	.2	.2	.2
Total	25.5	26.9	13.1	11.8	13.6	18.9	18.1

during 1933 and 1934; there was a slight gain in the total cover due to an increase in other grasses. The effects of the drought were first apparent in 1935 when the total cover was reduced to 13.1 percent. This was further decreased to 11.8 percent in 1936, after which there was a gradual increase to a maximum of 18.9 percent in 1938. There was a loss of less than 1 percent in 1939.

The relative degree of drought resistance of little bluestem and side-oats grama was clearly shown in comparing the reaction of each to its environment through the 7 years of drought. Little bluestem, which made up practically all the vegetation when the studies were begun in 1932, rapidly diminished until 1937 when a minimum cover of 4.3 percent was reached. The gain during 1938 and 1939 was small. Side-oats grama, on the other hand, gained rather steadily after its appearance in 1934 and constituted over 60 percent of the total vegetation in 1939.

OVERGRAZED CLOSED TYPE OF ANDROPOGON SCOPARIUS

Studies in the overgrazed little-bluestem type were begun in 1935, when the total cover had been reduced to only 11.5 percent (Table 10). The average cover

TABLE 10. Change in percentage of basal cover in 8 meter quadrats in an overgrazed closed type of *Andropogon scoparius* at Hays, Kansas.

Species	1935	1936	1937	1938	1939
Andropogon scoparius	3.1	1.4	.8	.5	.2
Andropogon furcatus	1.4	1.7	1.6	3.3	.7
Bouteloua curtipendula	3.4	3.3	7.7	11.5	12.1
Bouteloua gracilis	2.9	1.8	4.8	6.4	7.9
Bouteloua hirsuta	.6	.4	1.1	1.0	2.1
Buchloe dactyloides	....	.3	.5	3.2	4.3
Sporobolus cryptandrus	.1	.1	.6	.6	1.4
Aristida purpurea	....	.3	1.4	1.2	.8
Total	11.5	9.3	18.5	27.7	29.5

for any one species did not exceed 3.4 percent, and the lowest cover for any of the five most persistent species was 0.6 percent.

No quantitative determinations were made of the cover of the various grasses in this type before the drought, but notes from studies made on various occasions indicate that the total cover was only slightly less than on the ungrazed area. Due to reduced root extension and food storage in the crowns, the dominants under heavy grazing were unable to cope with drought as efficiently as when ungrazed. The reduced stature of the bluestems from grazing doubtless made possible the successful invasion of the short grasses such as blue grama, hairy grama, and buffalo grass. Even sand dropseed *(Sporobolus cryptandrus)* and wire grass became fairly well established in many of these areas (Fig. 18). The minimum cover of 9.3 percent was reached in 1936. The cover was practically doubled by 1937, and by 1939 it had reached 29.5 percent or more than three times that of 1936.

The two bluestems continued to decrease until their total cover was less than 1 percent in 1939. The increase of the more xeric grasses, side-oats grama, blue grama, hairy grama, and even buffalo grass, accounted for most of the gain. Side-oats grama, for instance, had 3.4 percent cover in 1935, but this had increased to 12.1 percent by 1939. Similar increases, though in smaller amounts, occurred in the other more xeric species.

CHANGES IN BUCHLOE-BOUTELOUA TYPE

These studies were begun in 1932 when several exclosures were made and numerous representative square meters selected for long-time study. They were extended in 1935, following 2 years of drought and a spring of exceptionally heavy dusting. It was at this time that areas ungrazed for many years,

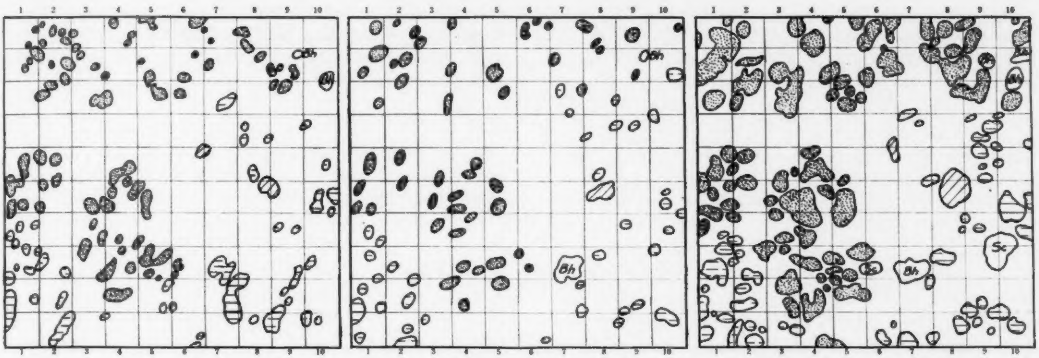

FIG. 18. Typical quadrat in overgrazed closed-type of *Andropogon scoparius* charted in 1935 (left), 1936 (center), and 1939 (right). Much of the little bluestem (horizontal hatch) had been killed by 1935 when its cover was only 1.8 percent. The space left bare by this grass was partially occupied by blue grama (small dots) and side-oats grama (broken horizontal hatch). Hairy grama (Bh) is also common in this location. *Aristida longiseta* (diagonal hatch) was present in only a small amount (0.4 percent) in 1935. Blue grama made steady gains under the influence of overgrazing and drought and had a cover of over 16 percent in the autumn of 1939. *Sporobolus cryptandrus* (Sc) invaded many of the open places during the drought.

some moderately grazed, and others that were overgrazed, were included.

The area of study was greatly increased in 1937. Quadrats were established to a distance of more than 200 miles southwest of Hays. The new pastures represented four general conditions: namely, lightly dusted and moderately grazed, lightly dusted and overgrazed, heavily dusted and lightly grazed, and heavily dusted and overgrazed.

UNGRAZED BUCHLOE-BOUTELOUA TYPE

The pasture under study in 1932 had been moderately grazed, but was thereafter protected from grazing. Determinations as to the relative proportion of the two dominants, blue grama grass and buffalo grass, were made in 1931 and 1932. They occurred in about equal abundance. As shown in Table 11A, the basal cover was 88.6 percent (Fig. 19). After 2

FIG. 19. Quadrat in the closed blue grama-buffalo grass type, typical of the short grasses in 1932 when they were only moderately grazed. The basal cover is 88.6 percent.

years of drought (1933 and 1934), the basal cover had been reduced to 84.7 percent. By 1935, the cover was further reduced to 65.4 percent and then to 57.7 percent in 1936. Thus, during the first 4 years of drought, reduction in basal cover was fairly slow.

TABLE 11. Change in percentage of basal cover in 10 meter quadrats in typical areas of the ungrazed Buchloe-Bouteloua type at Hays, Kansas.

A

Species	1932	1934	1935	1936	1937	1938	1939
Buchloe dactyloides ... / *Bouteloua gracilis*	88.6	83.7	64.9	57.7	8.7 / 15.8	15.6 / 15.0	9.3 / 13.0
Aristida purpurea	......	1.0	.5	......	.2	......	.....
Total	88.6	84.7	65.4	57.7	24.7	30.6	22.3

B

Species	Spring 1935	1935	1936	Spring 1937	1937	1938	1939
Bouteloua gracilis	20.3	18.9	9.1	13.8	16.1	23.4	21.1
Buchloe dactyloides	3.9	3.8	1.1	1.2	1.8	2.8	4.5
Sporobolus cryptandrus .	.5	.1	.0	.3	.3	.3	.3
Aristida purpurea	.2	.3	.4	......	.....	.....	.....
Agropyron smithii	.4	.2	.....	.1	.....	.....	.....
Total	25.3	23.3	10.6	15.4	18.2	26.5	25.9

The accumulated results of the drought produced the greatest breakdown in the cover between 1935 and 1937, and a cover of approximately 25 percent was reached in the fall of 1937. The amount increased to 30.6 percent in 1938 due to better growing conditions, but the drought of 1939 caused another decrease, and when charted in the fall only 22.3 percent of cover remained (Fig. 20) (Savage and Jacobson, 1935).

The basal cover of the vegetation on another area that had been ungrazed for many years before 1935 was significantly less than where moderate grazing was practiced prior to initiating this study (Table 11B). The excessive growth of the ungrazed vegetation during the favorable years evidently caused the grasses to be more susceptible to drought injury than were the moderately grazed ones.

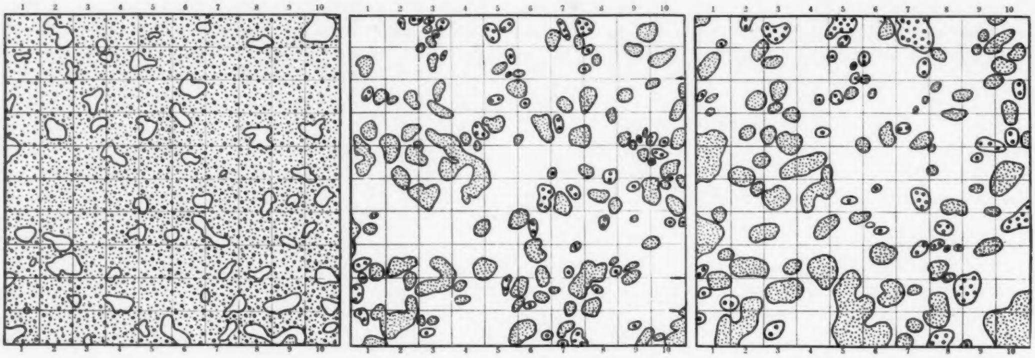

Fig. 20. Typical quadrat in ungrazed short-grass type with a dense cover, charted in the fall of 1932 (left), 1937 (center), and 1939 (right). Buffalo grass and blue grama grass were not charted separately in 1932; basal cover of the mixture was 89.5 percent. In 1937, the cover of buffalo grass (large dots) was 4.5 percent and that of blue grama grass (small dots) 16.2 percent. By 1939 the cover of these grasses had increased to 5.8 and 21.0 percent, respectively.

In the spring of 1935, the average basal cover was only 25.3 percent, most of which was blue grama. Buffalo grass, which had doubtless suffered greatest injury from drought, constituted only 3.9 percent of basal area. The remaining portion was divided among *Sporobolus cryptandrus, Aristida purpurea,* and western wheat grass *(Agropyron smithii).* Only a slight decrease occurred during the summer of 1935 and when charted in the fall the average cover was 23.3 percent. The greatest loss occurred between the fall of 1935 and that of 1936, when the cover was reduced to 10.6 percent.

Early spring growth in 1937 increased the cover to 15.4 percent but this amount was further increased to 18.2 percent during the remainder of the season. The cover was extended to 26.5 percent in 1938 and only slightly reduced during the season of 1939.

Comparisons made in other short-grass areas that were ungrazed indicated that in some instances the cover had increased to a percentage somewhat greater than that shown in Table 11. The ravages of the drought caused a great variation in the density of the vegetation. In some places, there occurred large barren areas almost devoid of plants. Hence, the numbers given in the table would seem to be somewhat below the average for 1938 and 1939 (Fig. 21).

The first signs of drought were observed early in June of 1933 when the immature staminate blossoms of buffalo grass were greatly damaged, and its leaves were spirally coiled and dead at the tips. The leaves of blue grama grass, though dark green in color, were rolled. They closely resembled those of Aristida. The immature inflorescences of squirreltail *(Sitanion hystrix)* were blasted by excessive heat. By June 15, the buffalo grass had become dormant in local areas where the supply of water was least. Elsewhere, however, the natural green color of the leaves was retained. Nearly all the blue grama and buffalo grass was dormant by July 1. The scattered bunches of little bluestem, wire grass, and squirreltail were badly withered and in many instances were nearly dead.

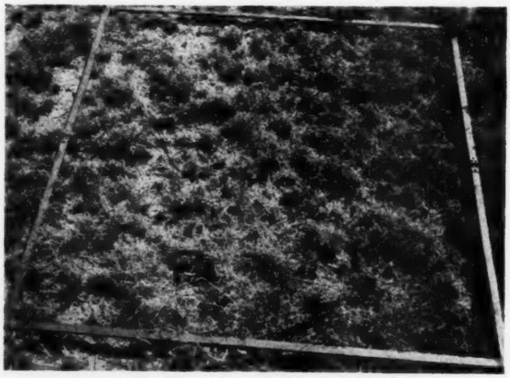

Fig. 21. View of ungrazed short grasses at Hays, Kansas, in 1939. The living basal cover has been reduced, during the past 7 years, to less than 30 percent.

A few scattered showers early in July supplied some available moisture for plant growth. Many of the grasses showed signs of life, especially in shallow depressions. Green color was restored in some instances where the leaves had not gone into complete dormancy. Usually, however, new leaves emerged from the crown, which was protected by the dormant vegetative cover; in fact, careful observations revealed that even in the periods of greatest drought small amounts of the crown remained green. Sufficient soil water was present during the third and fourth weeks of July to promote considerable plant growth. The small amount of moisture, however, was soon exhausted and by August 5, the grasses were again dormant. Growth was renewed late in August when the soil was moistened to a depth of approximately a foot.

Renewal of growth came late in the spring of 1934, due to the small quantity of available moisture. The rains in June, however, penetrated the soil to a depth of 2 feet and stimulated rapid development. This condition prevailed until early July, when the

drought became most severe. By the middle of July, all vegetation was badly wilted and many plants were completely dormant. They remained thus until rains late in August and early in September supplied sufficient moisture for growth.

It was during the drought of 1934 that the most exposed locations in this habitat suffered greatly. The bluish-gray color of the short grasses indicated that there were large areas where life was completely extinct. In other places, however, where the normal straw color was retained, the plants proved to be only dormant. It was further observed that areas suffering greatest losses were frequently occupied by a larger percentage of buffalo grass than blue grama grass.

Feeble growth of the two short grasses was observed late in March, 1935, where the layer of accumulated dust did not exceed 1 inch. This meager activity was reduced to almost nil during April when the greatest amount of dusting occurred. The rains of May, however, which were far above normal, washed away the dust and stored enough moisture in the soil to stimulate unusual plant activity. The stolons from the remnants of buffalo grass grew very rapidly. Early in June, when growing conditions were optimum, they often increased in length as much as an inch per day. It was not uncommon to find stolons 2 to 12 inches long rooted at the nodes where the cover was sufficiently open to permit them to make contact with the moist soil (Fig. 22). In some

FIG. 22. Photo at Phillipsburg, Kansas, showing open places in the short-grass cover caused by 2 years of drought. These were quickly reclaimed by stolons of buffalo grass in the spring of 1935. Most of the stolons were killed by the drought later in the season.

places, however, stolons were found to have grown one over the other until they had produced a carpet several inches thick. Under such circumstances, rooting at the nodes was impossible. Furthermore, it was frequently found that they grew over the dead remains of other grasses, which likewise prevented root development.

Numerous seedlings of buffalo grass and blue grama grass were scattered through the open places in the vegetation. Seedlings of six-weeks fescue (*Festuca octoflora*) were also found throughout the short grasses for the first time since 1932. On June 25, a few green sprouts were found growing from the borders of nearly dead bunches of wire grass. Buffalo grass stolons had become so abundant that they formed a heavy mat over much of the soil. By this time, many had reached lengths of 18 to 24 inches. The numerous small bunches of blue grama that survived the drought were now extending their cover by myriads of tillers (Riegel, 1940).

All short grasses, except those in depressions, were badly wilted by the middle of July. Many of the buffalo grass stolons, when shallowly rooted or when not in contact with the soil, had died back to the parent plant. The reactions of the grasses to the environmental conditions to which they were subjected indicated that under extremely adverse conditions the breakdown is rapid. Conversely, when conditions become favorable, replacement is equally rapid.

Growth was renewed during the latter part of March, 1936, and continued intermittently through May. The exceptionally dry months of June and July, however, forced all of the vegetation into dormancy and in many instances reduced the cover to nearly zero. In most places, the basal cover reached its minimum for the drought period in 1936, although the rains of August and September were sufficient to stimulate a small amount of fall growth.

The soil was extremely dry in the spring of 1937 and growth was not renewed until late May when the soil was moistened to a depth of 12 inches. This small supply of moisture was soon exhausted, and growth continued only intermittently until the rains of July supplied enough water to initiate the most vigorous growth of the season. By early July, a few dwarfed plants of *Festuca octoflora* were scattered throughout. The short grasses remained alive during August, but there was no apparent growth except in the more moist buffalo wallows and near the large drought cracks in the soil. The rains of late August provided some soil moisture and the grass which was scattered sparsely over the area produced short flower stalks early in September. Buffalo grass stolons also began growth, but this continued for only a short period.

The rainfall of April and May, 1938, was above normal, but due to excessive runoff only a comparatively small amount was stored in the soil. The short grasses began growth early in April and reached their maximum during late May and early June. By June 6, numerous buffalo-grass stolons, from 3 to 8 inches long, were radiating in all directions from the parent plants. Numerous tillers of blue grama grass were being added to the outside of the small tufts of living plants.

Myriads of buffalo grass and blue grama grass seedlings occupied the open spaces between the bunches of grass. It was not uncommon to find as

many as 10 to 25 per square foot. Growth continued with no interruption until early in July when the effects of drought became apparent. On July 18 many of the seedlings were dead. The tufts of mature grasses were dormant and many of the stolons of buffalo grass had died back to the place of their origin. The rains of late August and early September stored sufficient moisture in the soil to support the production of flower stalks of blue grama grass. Later study revealed, however, that a comparatively small percentage of caryopses were produced (Savage, 1937).

Early spring growth in 1939 was unusually weak. Light rains during April were insufficient to support active plant growth. During May, which was very dry, the vegetation became practically dormant. Rains in June, however, stimulated considerable activity which lasted until the first week in July, when the grasses again became dormant until the coming of showers in early August. Blue grama was in full head and buffalo-grass stolons were 4 to 8 inches long by the latter part of the month. Production of flower stalks on the blue grama, however, was again of no avail, since practically no caryopses were formed (Fig. 23). Side-oats grama and western wheat grass were commonly found in the buffalo wallows. A few bunches of *Aristida longiseta*, in full head, were scattered through the disturbed areas on the gentle slopes.

FIG. 23. Production of flower stalks of blue grama grass in the fall of 1939 on a moderately grazed area. Scarcely any of the florets contained caryopses.

MODERATELY GRAZED BUCHLOE-BOUTELOUA TYPE

Studies on the changes of the plant population were not limited to ungrazed areas. In the spring of 1935 meter quadrats were staked and charted in representative parts of a moderately grazed area. In October, 1935, the average percentage of basal cover was 49.2 (Table 12). This amount had been reduced

TABLE 12. Change in percentage of basal cover in 10 meter quadrats in a moderately grazed Buchloe-Bouteloua type at Hays, Kansas.

Species	1935	1936	1937	1938	1939
Bouteloua gracilis	49.1	3.9	7.0	15.9	14.4
Buchloe dactyloides		.4	1.7	4.6	12.3
Sporobolus cryptandrus	.1	.3	.2	1.8	1.1
Total	49.2	4.6	8.9	22.3	27.8

to 4.6 percent by the autumn of 1936, after which there were good gains through the 3 succeeding years. The total of 27.8 percent cover in 1939 was approximately 5 percent greater than that on the ungrazed area. This was due to an unusual increase in the cover of buffalo grass between 1938 and 1939. In some locations, however, the increase in cover of blue grama accounted for most of the gain between 1938 and 1939 (Fig. 24). The relative abundance of buffalo grass and blue grama grass was not determined separately until after 1935. Buffalo grass was reduced to its minimum of 0.4 percent in 1936. The more drought resistant blue grama grass fared somewhat better and had a cover of 3.9 percent. The response of the two grasses to drought was similar in other locations, buffalo grass suffering the greater loss and often almost disappearing except in buffalo wallows (Fig. 25). Upon the advent of better growing conditions, however, recovery was also much more

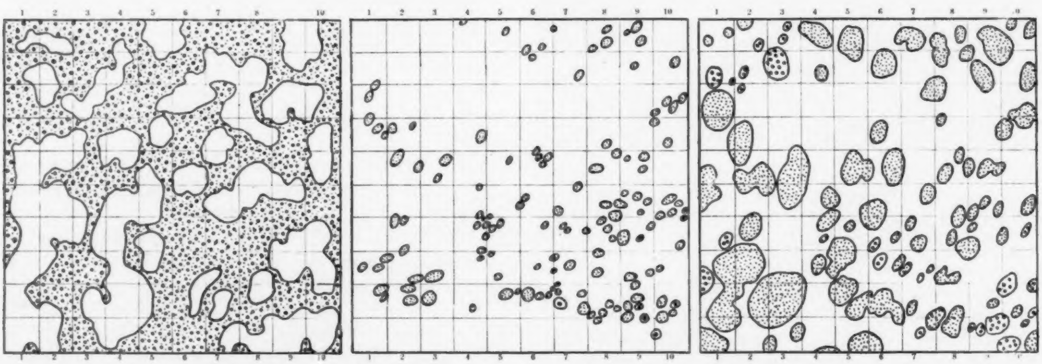

FIG. 24. Quadrat on moderately grazed short-grass type with dense cover. Cover of short grasses in the fall of 1935 (left) was 72.4 percent. A minimum cover of 0.15 percent of buffalo grass (large dots) and 2.8 percent of blue grama (small dots) was reached by 1937 (center). Significant gains were made by these grasses during 1938 and 1939 and, when charted in the fall of 1939 (right), buffalo grass had a cover of 3.1 percent and blue grama grass 24.2 percent.

FIG. 25. Short-grass cover at Hays, Kansas, late in August, 1937. Nearly all of the vegetation is blue grama grass, except that in the depression (center) where buffalo grass is abundant.

rapid; in fact, it was not uncommon for this species to increase its area from 3 to 10 times the original in a single season under optimum growing conditions.

Broken cover permitted the invasion of *Sporobolus cryptandrus*, which was present in only a small amount in 1935. The increase was not great but definite gains were made after 1937. The results of these studies indicate that moderate grazing is no great handicap to the normal development of the short grasses; in fact, there is reason to believe that moderate grazing under normal precipitation will produce a more uniform cover than that developed under total protection (Savage, 1939).

OVERGRAZED BUCHLOE-BOUTELOUA TYPE

Studies of an overgrazed short-grass type were made concurrently with those of one moderately grazed. In the fall of 1935 the basal cover on this type (22.1 percent) was less than half of that on the moderately grazed area (Table 13). The loss of both short grasses was extreme during the following year, the cover being only 2.6 percent in the fall of 1936.

TABLE 13. Change in percentage of basal cover in 7 meter quadrats in an overgrazed Buchloe-Bouteloua type at Hays, Kansas.

Species	1935	1936	1937	1938	1939
Bouteloua gracilis	9.1	1.9	4.9	7.0	10.0
Buchloe dactyloides	12.0	.5	1.8	5.0	8.3
Bouteloua curtipendula	.4	.1	.1	.4	.4
Triodia pilosa	.2	.1	.4	.5	.4
Sporobolus cryptandrus	....	....	.1	.4	.3
Andropogon furcatus	.4	....	....	....	....
Total	22.1	2.6	7.3	13.3	19.4

Areas 10 to 15 feet in diameter and containing nothing but a few scattered annual weeds were frequently found.

The cover was increased to 7.3 percent in 1937; to 13.3 percent in 1938; and further increased to 19.4 percent in 1939 (Fig. 26).

A few scattered plants of *Bouteloua curtipendula, Triodia pilosa,* and *Sporobolus cryptandrus* were found in some of the quadrats studied. *Andropogon furcatus* was present in a very small amount during 1935 in one quadrat where conditions were slightly more mesic than average. The intensity of grazing was materially reduced on these areas during 1938 and 1939; hence, recovery was more rapid than if they had been continuously overgrazed. The effects of overgrazing and constant dusting on the short grasses were little short of tragic. The cover was often reduced to less than 1 percent and growth was extremely weak (Fig. 27).

A comparison of the relative effects of the drought upon the Buchloe-Bouteloua type when subjected to different conditions is shown in Figure 28. The average basal cover on the area ungrazed since 1932 was better than that of the moderately grazed one, except in 1939. The cover in the overgrazed area was correspondingly lower than that of the moderately grazed one. Studies made in the spring of 1940 showed that the autumn and winter losses on the overgrazed areas far exceeded those of pastures that were moderately grazed or ungrazed. Data obtained

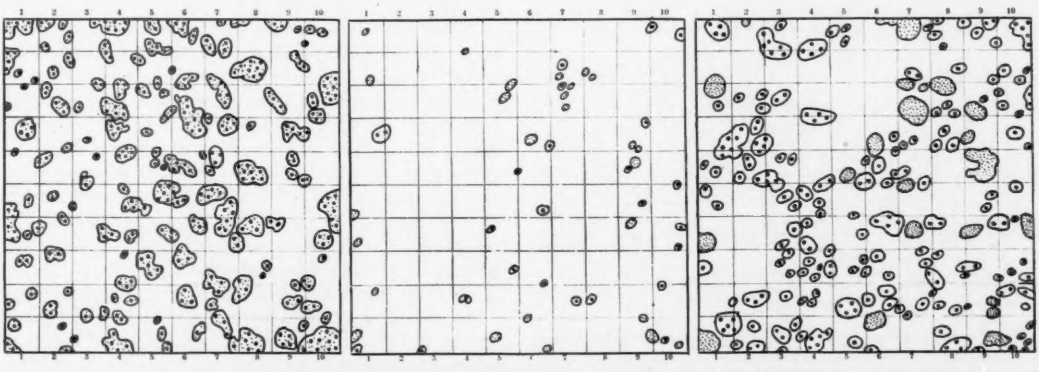

FIG. 26. Quadrat in typical overgrazed area of closed-type short grass. The buffalo grass (large dots) and blue grama (small dots) were not charted separately in 1935 (left), when the cover of the two grasses was 19.8 percent. The minimum of 0.84 percent was reached in 1936 (center). Note the rather uniform distribution of the surviving clumps throughout the quadrat. The basal cover increased to nearly 19.0 percent in 1939 (right).

FIG. 27. Range where grazing and continuous dusting has destroyed nearly the entire cover. Only a few scattered bunches, half covered with dust, remain. Hays, Kansas, 1939.

from several areas revealed that often as much as 75 percent of the 1939 cover had perished by the middle of May, 1940 (*cf.* Weaver and Albertson, 1940).

STUDIES IN THE ECOTONE

Studies on the change of vegetation were not limited to those of the typical little-bluestem and short-grass types, but extended through the transition belt which lies between these two habitats. Investigations were begun in the fall of 1932, and changes that have occurred subsequently have been closely followed. In places the transition from short grass to little bluestem was so abrupt as to make it possible to locate a meter quadrat so that it included a part of each type. Elsewhere, the little bluestem was scattered widely in bunches among the short grasses.

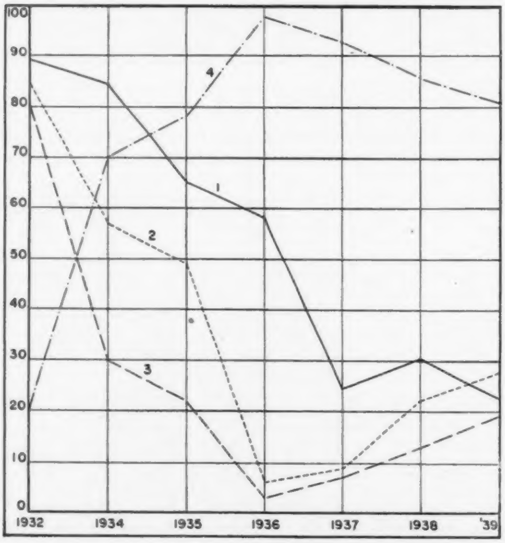

FIG. 28. Decrease in percentage of basal cover in a short-grass type: (1) ungrazed, (2) moderately grazed, and (3) overgrazed. The percentage of bare ground in the overgrazed range (4) reached its maximum in 1936.

LITTLE BLUESTEM-SHORT GRASS MIXTURE

In the fall of 1932, the average basal cover in quadrats located where there was a relatively large amount of little bluestem was 65.3 percent (Table 14A). Of this, 20.7 percent was buffalo grass and blue grama grass, and the remainder was big and little bluestem. The total cover was reduced to 49.3 percent by the fall of 1934, but had increased to 54.2 percent when charted in the fall of 1935. The most destructive effects of the drought occurred in 1936; the basal cover was then reduced to only 24.7 percent. Considerable increase occurred in 1937 and still more in 1938, and even the exceptionally dry year of 1939 produced a further increase, when the cover reached 51.3 percent (Fig. 29).

TABLE 14. Change in percentage of basal cover in 10 meter quadrats in an ungrazed area on the ecotone between the short grasses and little bluestem at Hays, Kansas.

A. Large amount of little bluestem.

Species	1932	1934	1935	1936	1937	1938	1939
Bouteloua gracilis	20.7	35.9	42.8	18.7	26.9	30.0	35.7
Buchloe dactyloides				1.6	4.2	9.3	12.2
Andropogon scoparius	40.1	10.1	5.7	1.6	.2	.....	.....
Andropogon furcatus	4.5	.8	.8	.5	.4	.1	.2
Bouteloua curtipendula ...	.....	2.5	4.9	2.3	2.3	2.4	3.2
Total	65.3	49.3	54.2	24.7	34.0	41.8	51.3

B. Small amount of little bluestem.

Species	1932	1934	1935	1936	1937	1938	1939
Bouteloua gracilis	76.2	74.0	68.5	50.5	21.3	21.9	29.2
Buchloe dactyloides					11.7	15.2	19.3
Andropogon scoparius	7.2	2.1	.9	.2	.....	.....	.....
Andropogon furcatus	.....	.1	.1	.0	.....	.....	.....
Bouteloua curtipendula ...	.....	.3	.0	.5	.4	.2	.0
Total	83.4	76.5	69.5	50.8	33.4	37.3	48.5

It is of interest that the chief dominant, little bluestem, which had a cover of 40.1 percent in 1932, rapidly descreased to 0.2 percent in 1937 and then disappeared. Big bluestem furnished 4.5 percent cover in 1932, but although it suffered considerable loss, very small amounts were found continuously throughout the 7 years. It was the increase in short grasses that prevented almost complete destruction of vegetation. In 1934, the cover of buffalo grass and blue grama grass had increased from 20.7 percent to 35.9 percent. A further increase to 42.8 percent occurred by the fall of 1935. This increase was caused by migration of the short grasses into the portions of the quadrats previously occupied by the bluestems and not by an actual increase in density in the parts which they originally covered.

The short grasses had spread throughout the quadrats by 1936, but the intense drought had reduced the cover of vegetation in a manner similar to that in other locations occupied by these species. It was this thinning out process that caused such an abrupt loss between 1935 and 1936. The increase from 24.7 per-

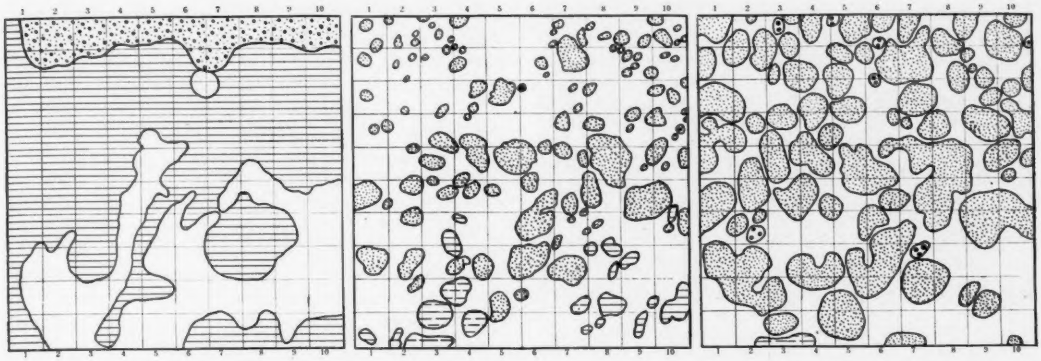

FIG. 29. Quadrat typical of the ecotone between short grasses and little bluestem. The short grasses (dots) formed a dense cover over one side of the area in 1932 (left). The remainder was occupied by little bluestem (horizontal hatch). The open space is bare ground. As the drought continued, little bluestem was all killed and replaced by short grasses and side-oats grama (broken horizontal hatch). The cover was reduced from 71 percent in 1932 to 19 percent in 1936 (center). By 1939 (right) it had increased to 51 percent, due primarily to an excellent growth of blue grama grass.

cent of basal cover in 1936 to 51.3 percent in 1939 was made possible by the gradual spread of both short grasses. Blue grama grass nearly doubled its cover, and buffalo grass, which was reduced to 1.6 percent in 1936, increased its holdings to 12.2 percent—more than seven times its minimum. Side-oats grama, which was absent in 1932, afforded 2.5 percent of the cover in 1934. No large gains of this grass occurred, but its persistence indicates a greater drought resistance than that of the two bluestems.

In areas where little bluestem constituted a small percentage of the vegetation in 1932 (Table 14B), the change in cover was considerably different from that in the more mesic locations where the little bluestem was relatively heavy. The average total cover in the fall of 1932 was 83.4 percent. The decrease was gradual thereafter until 1937, when the minimum of 33.4 was reached. By the fall of 1938 it had increased to 37.3 percent, and to 48.5 percent in 1939. Since little bluestem formed only a small percentage of the vegetation in the beginning, the total cover was not changed appreciably by its replacement with the more xeric short grasses.

The short grasses covered 76.2 percent of the area charted in 1932. They lost slightly in 1934, and a little more in 1935 when the cover was reduced to 68.5 percent. The extreme drought of 1936 reduced the basal area of short grasses to 50.3 percent, and further reduction occurred in 1937 when it reached its minimum of 33.0 percent. Each of the short grasses made gains thereafter. Both bluestems disappeared in 1936. Side-oats grama, which appeared first in 1934, was never present in any considerable amounts.

SIDE-OATS GRAMA-SHORT GRASS MIXTURE

Side-oats grama had evidently invaded the short grasses during the wet period previous to the drought. It constituted the major portion of the vegetation in local areas on the more xeric side of the ecotone between the little-bluestem and the short-grass habitats. Several permanent quadrats representative of this condition were charted in the fall of 1932 (Table 15). The total cover was 81.8 percent. This amount was diminished to 74.7 percent in 1934 and to 47.9 percent in 1935. The minimum of 14 percent was reached in 1936. The gain in cover thereafter was relatively rapid and by 1939 it was 44.9 percent.

TABLE 15. Change in percentage of basal cover in an ungrazed area occupied by side-oats grama and short grasses in 1932 at Hays, Kansas.

Species	1932	1934	1935	1936	1937	1938	1939
Bouteloua curtipendula	60.2	50.5	21.7	3.3	5.9	2.7	4.3
Bouteloua gracilis }	21.6	24.0	26.0	5.7	15.9	15.0	19.0
Buchloe dactyloides }				4.8	11.9	17.4	20.5
Andropogon furcatus	.....	.....	.....	.1	.3	.2	.1
Aristida purpurea	.....	.2	.2	.....	.....	.....	.....
Sporobolus cryptandrus	.....	.....	.....	.1	.7	.9	1.0
Total	81.8	74.7	47.9	14.0	34.7	36.2	44.9

The behavior of side-oats grama in this location was similar to that of the little bluestem farther down the slope. This grama grass, with a cover of 60.2 percent in 1932, rapidly decreased to only 3.3 percent in 1936. It gained slightly in 1937, but reached its minimum of 2.7 percent in 1938, and then increased to 4.3 percent in 1939.

The short grasses, which had 21.6 percent cover in 1932, increased to 26 percent in 1935. This cover was reduced to only 10.5 percent in 1936. The gains were constant thereafter and by the fall of 1939 these two grasses occupied nearly 40 percent of the area.

MIXED MID GRASSES AND SHORT GRASSES

In 1934 it was observed that the more mesic grasses, such as little bluestem and wire grasses that were scattered through the short grasses on the nearly level tablelands, had suffered exceptionally

heavy losses. Permanent quadrats were located and charted to show the cover in 1934 after 2 years of extreme drought. The average cover where little bluestem was the dominant mid grass was 33.6 percent (Table 16A). The cover was reduced to 21.8 percent in 1935 and to only 9.5 percent in 1936. A gradual increase occurred during the next 3 years, and a total of 35.2 percent was present in 1939. The 19 percent of little bluestem in 1934 had decreased to 0.5 percent in 1935 and was absent thereafter. Side-oats grama suffered a similar fate. The two short grasses had a cover of less than 6 percent in 1934. They increased to slightly over 18 percent in 1935, but were reduced to 9 percent in 1936. Basal cover of blue grama grass changed from 8 percent in 1936 to 30.3 percent in 1939. Buffalo grass likewise increased from 1 percent to 4.9 percent during the same period.

Table 16. Change in percentage of basal cover in a moderately grazed area occupied (A) by little bluestem and short grasses, and (B) by wire grass and short grasses at Hays, Kansas.

A

Species	1934	1935	1936	1937	1938	1939
Andropogon scoparius	19.0	.5				
Bouteloua curtipendula	7.2					
Bouteloua gracilis	4.3	13.0	8.0	18.4	26.0	30.3
Buchloe dactyloides	1.4	5.2	1.0	4.4	8.5	4.9
Aristida purpurea	1.7	3.1	.5			
Total	33.6	21.8	9.5	22.8	34.5	35.2

B

Species	1934	1935	1936	1937	1938	1939
Bouteloua gracilis } *Buchloe dactyloides* }	24.4	25.9				
Bouteloua gracilis			4.6	14.3	18.6	19.7
Buchloe dactyloides			1.5	5.4	13.5	6.9
Aristida purpurea	7.8	1.4	.1			
Total	32.2	27.3	6.2	19.7	32.1	26.6

The two wire grasses (*Aristida purpurea* and *A. longiseta*) were commonly found in local weedy areas on gentle slopes in 1934, when studies concerning the behavior of these grasses were begun (Table 16B). The first year the total cover was 32.3 percent, 7.8 percent of which was wire grass and the remainder, 24.4 percent, short grasses. The cover of wire grass rapidly decreased and by 1936 only remnants remained. Observations in areas adjacent to those of intensive study indicated that this grass was reduced to less than 1 percent throughout the area. A few scattered plants were found growing in local weedy places in 1938; although none were present in the quadrats that were charted.

Changes in the Andropogon furcatus Type

Great changes also occurred in the big bluestem type which characterized the larger ravines and most mesic slopes. At the beginning of drought in 1933 big bluestem constituted about 75 percent of the vegetation. Species of less importance included *Bouteloua curtipendula,* wild rye grass *(Elymus virginicus)* and long-leaved dropseed *(Sporobolus asper hookeri).*

Decrease in available soil moisture in this habitat lagged behind that of the little-bluestem and short-grass types; hence, the changes in the composition and abundance of the vegetation were slower to appear. The change, at first, was one of shifting in the relative amount of the various native grasses rather than an actual decrease in the total cover. Later, however, as the available soil moisture decreased and as the amount of loose soil washed in from the partly bared watersheds increased, the plant population was materially reduced. All of the more mesic grasses decreased both in size and abundance. These included big bluestem, tall panic grass *(Panicum virgatum),* Indian grass *(Sorghastrum nutans),* wild rye grass *(Elymus virginicus),* and plains bluegrass *(Poa arida).* The more xeric grasses, however, such as western wheat grass, side-oats grama, and long-leaved dropseed, made definite gains. Western wheat grass, a species immediately bordering the ravines, invaded the lowlands from this vantage point, and long-leaved dropseed spread from small areas of nearly pure stands in the heads of ravines.

Debris of soil and dead plants washed down from above and often covered much of the vegetation, thus creating bare areas. These were usually populated by myriads of such weedy annuals as the common sunflower *(Helianthus annuus),* lamb's quarters (mostly *Chenopodium album*), and Russian thistle *(Salsola pestifer).* While none of the species entirely disappeared, a loss of fully 25 percent of the vegetation resulted from the combined influences of drought and consequent soil erosion and deposit.

Studies in Southwestern Kansas

Studies of the effects of the drought on the vegetation were considerably expanded in 1937 by placing meter quadrats in representative areas at 15 different stations in southwestern Kansas (Fig. 1). Each quadrat was recharted in 1938 and again in 1939, and studies were made as to the general condition of the surrounding vegetation. The results are grouped according to the conditions to which the area was subjected at the time of the initial quadratting. The amount of subsequent dusting has varied somewhat, but the classification is reasonably accurate. Condition 1 indicates light dusting and moderate grazing; 2, light dusting and overgrazing; 3, heavy dusting and moderate grazing; and 4, heavy dusting and overgrazing (Table 17).

The basal cover in 1937 varied from 10.0 to 32.9 percent under condition 1 and averaged 19.8 percent. The average was increased to 27.8 in 1938, a gain which was again lost during the drought of 1939 (Fig. 30). The relative proportion of buffalo grass and blue grama varied considerably and generally no apparent reason could be found for the differences. At three of the four stations, the percentage of buffalo grass cover averaged much higher than that of blue grama grass. At Scott City, the reverse was true. At Oakley, there was a large gain in buffalo grass between 1937 and 1938 and then an enor-

TABLE 17. Deviation from mean precipitation, condition, percent of basal cover of blue grama grass and buffalo grass, and basal cover on representative pastures near each station.

Year	Precipitation	Condition*	Blue grama grass	Buffalo grass	Total	Precipitation	Condition*	Blue grama grass	Buffalo grass	Total	Precipitation	Condition*	Blue grama grass	Buffalo grass	Total
	Quinter					Oakley					Deerfield				
1937...	-8.0	1	3.9	29.0	32.9	-4.5	2	4.4	.2	4.6	- 5.2	3	4.9	1.4	6.3
1938...	-1.6	1	.8	27.8	28.6	+2.1	2	17.5	2.8	20.3	- 4.2	3	5.2	4.4	9.6
1939...	-5.0	1	2.2	35.3	37.5	-6.6	2	16.0	3.7	19.7	- 9.0	3	3.9	4.0	7.9
	Oakley					Quinter (Av. 3 Quads.)					Syracuse				
1937...	-4.5	1	6.4	14.3	20.7	-8.0	3	2.2	1.6	3.8	- 9.3	3	3.9	2.2	6.1
1938...	+2.1	1	10.1	29.9	40.0	-1.6	3	3.4	2.9	6.3	- .7	3	4.3	6.3	10.6
1939...	-6.6	1	5.4	5.0	10.4	-5.0	3	9.4	7.7	17.1	- 9.6	3	2.8	11.7	14.5
	Scott City					Oakley					Tribune				
1937...	....	1	14.3	1.3	15.6	-4.5	3	2.1	1.4	3.5	- 4.9	4	1.5	0.0	1.5
1938...	....	1	10.3	5.4	15.7	+2.1	3	7.0	9.1	16.1	+ 2.9	4	1.7	0.0	1.7
1939...	....	1	9.0	1.7	10.7	-6.6	3	8.0	17.7	25.7	- 4.0	4	5.2	0.0	5.2
	Marienthal					Ness City (Av. 4 Quads.)					Holcomb				
1937...	-4.0	1	1.7	8.3	10.0	-7.9	3	2.5	1.8	4.3	-11.4	4	.9	1.1	2.0
1938...	- .6	1	2.0	24.7	26.7	- .9	3	7.3	6.0	13.3	- 4.8	4	0.0	0.0	0.0
1939...	-2.7	1	1.7	15.7	17.4	-7.0	3	9.4	8.4	17.8	- 9.8	4	0.0	0.0	0.0
	Quinter					Dighton (Av. 2 Quads.)					Syracuse				
1937...	-8.1	2	5.1	1.4	6.5	-7.4	3	5.2	5.6	10.8	- 9.3	4	0.0	0.0	0.0
1938...	-1.6	2	11.9	4.6	16.5	-4.1	3	6.8	5.7	12.5	- .7	4	0.0	0.0	0.0
1939...	-5.0	2	17.1	14.9	32.0	-8.3	3	3.9	2.5	6.4	- 9.6	4	0.0	0.0	0.0

*Condition at time quadrats were laid out in 1937: 1, lightly dusted, moderately grazed; 2, lightly dusted, overgrazed; 3, heavily dusted, moderately grazed; and 4, heavily dusted, overgrazed.

FIG. 30. Meter quadrat in a lightly dusted and moderately grazed short-grass pasture near Marienthal, Kansas. The total cover in August, 1939, when the photograph was taken, was 17.4 percent.

mous loss in 1939. The rainfall deficit for 1939 at Oakley was 6.6 inches, but it was 2.1 inches above normal in 1938. This readily explains the loss that occurred between 1938 and 1939. At Quinter, there was a gain between 1938 and 1939 in spite of a greater rainfall deficit during the latter year (Fig. 31). It seems that the ability of buffalo grass to endure dry periods depends upon the depth to which the roots arising from the stolons have penetrated when drought begins.

Under light dusting and overgrazing (condition 2), the average cover was 5.5 percent in 1937. This was

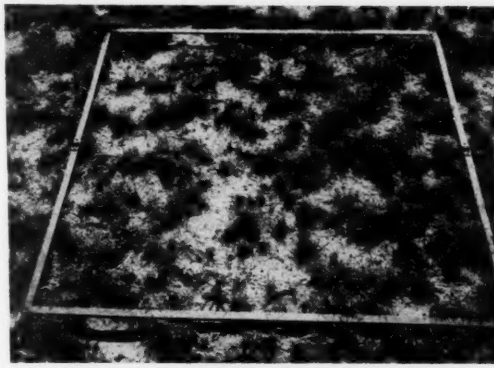

FIG. 31. Meter quadrat in a lightly dusted and moderately grazed short-grass pasture near Quinter, Kansas. The cover in 1939 was 37.5 percent. Photo in September, 1939.

increased to 18.4 percent in 1938 and to 25.9 percent in 1939. Oakley had a cover of 19.7 percent and Quinter, 32.0 percent in 1939 (Fig. 32). The relatively large cover at Quinter in 1939 resulted from a great increase in the cover of buffalo grass.

When the area was heavily dusted and moderately grazed (condition 3), the average percentage of basal cover was 5.8 in 1937. It increased to 11.4 percent in 1938 and then to 14.9 percent in 1939 (Fig. 33). Cover was shared about equally by the two short grasses except at Oakley, where the buffalo grass had a cover of 17.7 percent in 1939, as compared with 8 percent for blue grama.

Vegetation under condition 4, where the grass was heavily dusted and overgrazed, suffered greatest from the drought. The average cover in 1937 was 1.2 percent. In 1938 it was reduced to 0.6 percent, and in 1939, it had increased to only 1.7 percent. Several of these areas contained no vegetation at all except an occasional forb or ruderal. The cover of vast areas of native prairie, because of severe dusting and

FIG. 32. Meter quadrat in a lightly dusted and overgrazed pasture near Quinter, Kansas. The basal cover in 1939 was 32 percent. Photo, Sept. 5, 1939.

FIG. 33. Meter quadrat in a heavily dusted and moderately grazed pasture near Quinter, Kansas. The cover in the autumn of 1939 was 15.7 percent. Photo, Sept. 5, 1939.

overgrazing, has been reduced to nearly zero (Fig. 34). This type of prairie constitutes a large portion of the grassland near the center of the dust bowl. Farmers report that many of the dust storms since 1935 have arisen in these prairies. Drifts of soil, often 30 inches high and extending for many rods, are frequently found in this region.

The yield of palatable forage in overgrazed pastures is less than 10 percent of that produced in well-managed ones. This fact is exceedingly important when considering the rate of stocking the range. Many ranges originally stocked at the rate of one animal unit to 10 to 12 acres now require 30 to 50 acres to support one animal. This condition has placed an exceedingly difficult task upon ranchers since it has often been practically impossible to produce supplementary feeds such as sorghums. As a consequence, they have been compelled to dispose of most of their livestock, thereby greatly reducing the farm income and making the earning of an independent living almost impossible. It seems clear that several years of normal or above normal precipitation with the most judicious range management will be necessary to restore the former cover of grasses.

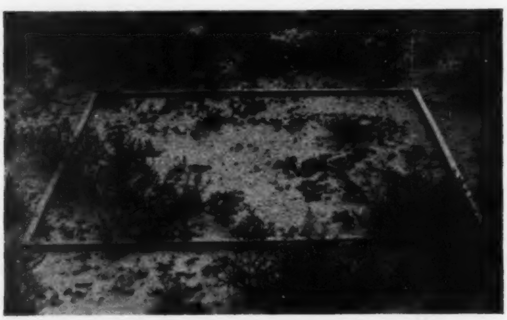

FIG. 34. Meter quadrat in a heavily dusted and overgrazed pasture near Holcomb, Kansas. Only the dead crowns of the native grasses remain to distinguish it from the adjacent cultivated fields. Most of the weeds are *Salsola pestifer*. Photo, July 27, 1939.

SUMMARY

The prairie vegetation of western Kansas has been studied through 7 years of continuous drought, 1933 to 1939, inclusive. Investigations were centered at Hays, but studies were made in many counties. Water content of soil has been determined weekly during the growing season, and a record of aerial environmental factors obtained. Reactions of the mixed prairie and short grass vegetation have been recorded year by year in scores of permanent, widely distributed quadrats, and by extensive field notes.

The pioneers found a dense cover of vegetation. They broke only enough sod to grow crops for food, and winter forage and grain for their livestock. Farming, which for a long time was incidental to stock raising, received a great impetus with the invention of labor-saving machinery and a period of high prices for wheat. Despite this stimulus to agriculture, over one third of the land remains unbroken. Saturation of the wheat market turned attention to livestock production just at a time when the range was severely depleted by drought and dust coverage. Extent of grassland was limited and overgrazing and deterioration inevitable.

Moderately grazed and ungrazed prairies were in excellent condition in 1933 because of a very favorable six-year period just preceding when the average annual precipitation (27.8 in.) was approximately 5 inches above normal.

Annual precipitation during each of the drought years was below normal and during 4 of the 7 years nearly 7 inches below. Most of this deficit occurred during the growing season. Periods of 5 to 7 weeks in summer with practically no rainfall occurred. An accumulated deficit of 6.7 inches in 1933 increased to 21.6 in 1936 and to 34.5 inches in 1939.

Temperatures were abnormally high during the drought and duration of periods with high temperatures unusually long. Average daily maximum temperatures for June, July, and August of the 4 driest years were 93.2°, 100.6°, and 94.8°F., respectively, or 8.0°, 7.5°, and 4.4° higher than for the same months during 1925-1932.

Wind movement was abnormally high. That of 1934 was greatest, being 41,782 miles from April to September, inclusive. The lowest (1936) was 33,838 miles. The highest wind movement occurred in April and May and often resulted in great dust storms. Combined effects of cultivation, overgrazing, and drought created conditions extremely conducive to dust storms. Such storms were frequent but not severe during 1932. Many dust storms of wide extent occurred in April, 1933, but the blowing of dust reached a climax in March and April of 1935. Sometimes the storms were of several days duration. Vast areas of vegetation were smothered by thin blankets of silt or by great drifts of loose earth. After the

vegetation died, the dust was again moved by the wind and thus supplied the silt for later black blizzards.

The average seasonal evaporation (April to September, inclusive) from a free water surface was 48.5 inches preceding the drought. It was always greater during the drought and was 66.4 inches in 1934. Average monthly evaporation for the drought years was 1.8 inches higher than normal in June, 2.7 inches in July and 1.7 inches in August, and was 8.5 inches above normal for the growing season.

Water content of soil was determined at weekly intervals throughout the growing season to a depth of 5 feet. Available water was the limiting factor to plant production. There was about 2 percent residual water available to plants at certain depths below 2 feet in 1933 but none thereafter. Water was nonavailable in the second foot after the first week in June, 1933, and continuously so except for 2 weeks in June, 1934, and during the entire month in 1935. From 1937 to 1939, inclusive, the second foot of soil had no water available for plant growth. Even water in the surface foot was depleted to an amount nonavailable for growth during three 2-week periods in 1933, one 4-week period in 1934, and one 7-week interval in 1935. This occurred when water was also nonavailable at any depth to 5 feet, and the plants succumbed or became dormant. During 3 separate weeks in 1937 they were without available water; similar periods of 2 and 5 weeks duration occurred in 1938, and in 1939 there were three, including one of 4 weeks duration in July and August.

Three types of vegetation, with varying degrees of intermixtures, are common in the mixed prairie of west-central Kansas. They are the little bluestem *(Andropogon scoparius)* type, common on hillsides and in shallow ravines; the short-grass (Buchloe-Bouteloua) type, widely distributed over nearly level uplands; and the big bluestem *(Andropogon furcatus)* type of larger ravines and lower moist slopes.

During the 7 years of drought, vegetation remained wilted or dried over periods of several weeks duration. Periods of dormancy alternated with those of growth several times during a single summer. Many mesic plants disappeared completely and even the most xeric species were reduced greatly in numbers. Animal life was also greatly depleted.

The complete story of the deterioration of the little bluestem type has been recorded. The original basal cover of about 60 percent was composed of approximately one-sixth big bluestem and nearly all of the remainder was little bluestem. Even where protected from grazing, little bluestem decreased so rapidly that only 10 to 20 percent remained in 1935, and 1 to 4 percent in 1939. Big bluestem was reduced to 2 percent or less. Invasion of more xeric species, especially side-oats grama *(Bouteloua curtipendula)* and blue grama *(B. gracilis)* resulted in the minimum basal cover of 16 percent (1936) being increased to 22 to 30 percent in 1939. Accumulated benefits derived from the best drought years were often expressed by better growth the following season, even if dry. Myriads of seedlings sometimes appeared in the open spaces between the living bunches but nearly all succumbed. Opportune showers permitted flowering of mature plants but few viable seeds were produced.

Late in the drought period, large areas of level prairies were found to be completely devoid of little bluestem. Some big bluestem survived owing not only to its greater depth of root system but also to the large amounts of reserve foods in crowns and rhizomes. Side-oats grama, once established in the bared areas, spread considerably, mostly by short rhizomes, the young shoots from them surviving more severe drought than the seedlings. Plants of blue grama grass increased by tillering. The increase was slow but constant in the little bluestem habitat.

In the ungrazed open type, the predrought basal cover was often only 25 percent, and consisted of nearly pure little bluestem. It was reduced rapidly after 1934, and to 12 percent in 1936. Increase of side-oats grama, which became dominant, from 4 to 11 percent, partly counterbalanced the losses suffered by little bluestem. Basal cover was about 18 percent in 1939.

Basal cover in the overgrazed little bluestem type had been reduced to 11.5 percent in 1935. Side-oats grama and blue grama constituted about half of the cover, which reached its minimum of 9.3 percent the next year. Although the bluestem all but disappeared, the total vegetation, including buffalo grass, improved steadily and attained a basal cover of 30 percent in 1939.

Studies in the Buchloe-Bouteloua type were begun in 1932 and extended in 1935 to include several grazing treatments. In 1937 quadrats were established in pastures in 10 different counties of western Kansas; some pastures had undergone various degrees of covering by dust.

Ungrazed pastures, formerly moderately grazed, with an approximately equal mixture of buffalo grass *(Buchloe dactyloides)* and blue grama grass in almost pure stands presented a basal cover of 80 to 90 percent. This decreased slowly until 1936 when it was only 58 percent, and the next year to 25 percent. Although fluctuating somewhat, this stand was further reduced to 22 percent in 1939.

Deterioration was much greater in a similar, adjacent pasture that had been ungrazed for many years. Excessive growth of the vegetation during the good years preceding drought made it more susceptible to drought injury than pastures which had been moderately grazed. Basal cover was only 25 percent in 1935, and 11 the next year. Thereafter there was a slow but steady improvement until 1938-39 when it was again 26 percent. There was little change in composition of the vegetation, although previous to 1935 buffalo grass had suffered the greater loss. In portions of the pasture there were large areas almost without vegetation. Areas suffering the greatest losses had been composed more largely of buffalo

grass than blue grama. Where local dust deposits exceeded ½ inch in depth the short grasses were handicapped and a cover an inch or more in depth was usually fatal.

Despite quantities of seedlings, and rapid propagation of buffalo grass by stolons in 1935 and at other times, periods favorable for growth were usually too short to result in establishment. Flower stalks were sometimes formed, but few seeds matured. With dusting and denudation, rainfall became less efficient and runoff greatly increased.

In the short grass type moderately grazed during the drought, an average basal cover of about 50 percent was found in 1935. This was reduced to about 5 percent in 1936, less than ½ percent being buffalo grass. It then gradually increased to 28 percent by 1939. In some areas buffalo grass, which often remained only in shallow depressions, increased more rapidly, in others, the more drought-resistant codominant, blue grama grass. Few other species were even of minor importance.

Overgrazed short grass ranges were reduced to a cover of 22 percent or less than half of that under moderate grazing. Blue grama grass was reduced to 2 percent, buffalo grass to less than 1 percent, and the total basal cover to about 2.5 percent when most depleted in 1936. Areas 10 to 15 feet in diameter and entirely bare of grass were frequent. Recovery was aided by reduced grazing pressure and basal cover increased year by year to 7, 13, and 19 percent.

Basal cover in ungrazed, moderately grazed, and overgrazed short grass ranges (where the cover in 1932 varied from 88 to 80 percent, respectively), was reduced in a somewhat parallel manner. Maximum reduction was least and a year later in ungrazed grassland. Percentages of cover were, in order, 65, 48, and 22 in 1935 but 58, 7, and 3 in 1936. By 1938 the cover was 31, 22, and 13 percent, respectively. Further heavy losses on overgrazed ranges were recorded in 1940.

The transition area between the little bluestem and short grass exhibited several mixtures. Even where large amounts (40 percent) of little bluestem were found, total loss of the species usually occurred. Total basal cover was reduced from 65 to 25 percent. Owing to the entrance of side-oats grama and to a great increase of short grasses, about 50 percent cover was present in 1939.

Drought over most of the range area, except where it was accompanied by dust burial, resulted in severe thinning of the short grasses rather than their complete destruction.

Side-oats grama was intermixed with short grasses in more xeric situations in the ecotone before the drought. Where it constituted 60 percent of the cover in 1932, it decreased to 3 percent by 1936 and scarcely gained thereafter. The short grasses, about equally intermixed, were more resistant to desiccation. They decreased from 22 to 11 percent, but by 1939 doubled their original basal area. Thus, the total basal cover of 82 percent (1932) was reduced to 14 in 1936 but was 50 percent in 1939.

Where several mid grasses, including wire grasses (*Aristida purpurea* and *A. longiseta*), were intermixed with short grasses in the transitional area, all disappeared in 1 to 3 years. The short grasses were at a low ebb in 1936 but subsequently regained the ground lost by the mid grasses, so that the initial basal cover of 34 percent was again attained.

Great changes also occurred in the big bluestem type, although decrease in available soil moisture was slower here as was also decrease in abundance of vegetation. Western wheat grass *(Agropyron smithii)*, side-oats grama and other more xeric grasses partially replaced big bluestem, tall panic grass *(Panicum virgatum)*, and other mesic species. A loss of one fourth of the vegetation resulted from drought and consequent soil erosion and deposit.

Intensive studies of ranges were made in ten additional counties in western Kansas, beginning in 1937. All were in the short grass type. On lightly dusted and moderately grazed ranges basal cover varied from 10 to 33 percent. Percentage of buffalo grass usually averaged higher than that of blue grama. Variations in cover were usually closely correlated with the amount of rainfall. No permanent gains occurred by 1939.

Under light dusting and overgrazing a cover of 5.5 percent increased to 18 in 1938 and to 26 in 1939. At some stations this resulted from an excellent growth of buffalo grass. Where heavy dusting and moderate grazing occurred and buffalo grass and blue grama were about equally represented, the basal cover of 6 percent increased to 15.

Vegetation suffered the greatest losses under heavy dusting and overgrazing. An average basal cover of 1 to 2 percent showed no increase by 1939. This much-depleted type of grassland is of very wide distribution and constitutes a large portion of the vegetation near the center of the dust bowl.

Drought, overgrazing, and hordes of grasshoppers have caused great reduction in carrying capacity of the range. Yield of palatable forage in overgrazed pastures is less than 10 percent of that produced in well-managed ones. Where 10 to 12 acres was formerly required to sustain one animal unit, 30 to 50 acres are now needed.

Several years with normal or above normal precipitation and with the most judicious range management will be required to restore the former cover of grasses.

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AN ECOLOGICAL STUDY OF THE VEGETATION OF SOUTHEASTERN WASHINGTON AND ADJACENT IDAHO

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AN ECOLOGICAL STUDY OF THE VEGETATION OF SOUTHEASTERN WASHINGTON AND ADJACENT IDAHO

INTRODUCTION

The vegetation of the unforested regions in the Pacific Northwest has been less thoroughly studied and is consequently less perfectly understood than is that of the forested areas. Five citations (Weaver 1914, 1915, 1917; Shantz 1924; Daubenmire 1940) constitute a practically complete bibliography of published researches on the natural plant communities of the great expanse of open country with which the present study is concerned.

Agricultural development began in southeastern Washington only about 50 years ago (Strahorn *et al.*, 1929) but its expansion has been so rapid and complete that few typical remnants of the original prairie and desert remain. These relics of the primeval vegetation likewise seem to be heading toward nearly complete extermination within a few years, so that the time is opportune for obtaining statistical records of these communities. Moreover, as the irrigation project connected with the Grand Coulee Dam is developed, a better understanding of the natural vegetation types of the Big Bend area should find practical application in land classification.

The area covered by the present survey is limited on the east by segments of the Snake and Clearwater Rivers, and by the forested foothills of the Bitterroot Mountains. The north and west boundaries follow the Spokane and Columbia Rivers, and the southern edge is determined by the southern boundary of Washington and the forested slopes of the Blue Mountains (Fig. 1).

The desert-like western half of this area lies in a great bend of the Columbia River, and is locally referred to as the "Big Bend" country. The eastern half, the prairie region which borders the Bitterroots from Spokane to the Blue Mountains, is widely known as the "Palouse region." The term Palouse is believed to have been derived from the French *pelouse,* meaning lawn or greensward, and to have been first applied to the region by early Jesuit missionaries (Rees, 1918). A century ago, trappers referred to this unforested plain as the "plateau of the Spokane" (Van Osdel, 1915, p. 160). Physiographically it is known as the Walla Walla section of the Columbia Plateau (Fenneman, 1931).

The aim of the present study is to enumerate and characterize the principal natural plant associations of the region, to indicate the particular portion of the region covered by each, and to point out some of the environmental factors which may control this vegetational pattern. Three years of intermittent study are obviously too few to permit a complete study of so large an area. Consequently some phases have been greatly neglected while others, such as the analyses of the upland prairies, have received the major share of attention.

The writer wishes to acknowledge the assistance rendered by the Northwest Scientific Association in supporting a part of these field studies with research grants in 1937, 1938, and 1939. The willing and capable assistance of Jean B. Daubenmire in the field has also been of great value.

ORIGIN OF TOPOGRAPHY AND SOILS

Most of the present topography and soils of southeastern Washington have originated since Oligocene time. At some point between late Oligocene and mid-Miocene, there began a series of lava flows (early effects of the Cascadian Revolution) which were ultimately to cover all of southeastern Washington and much of the surrounding region (Fenneman, 1931). Welling up quietly from fissures and a few vents, the molten lava spread out in thin layers before cooling. As the deep valleys of the older topography became filled by successive lava extrusions, even the highest ridges disappeared and a flat basalt plateau, the Columbia Plateau, developed. An area totaling nearly 52 million hectares and occupying parts of Washington, Oregon, and Idaho was inundated in this manner by successive emissions of lava which occurred intermittently until early Pleistocene.

This basaltic plain extended northward to the Okanogan Highlands of northern Washington, eastward to the foothills of the Bitterroot Mountains of Idaho, westward into the region which is now occupied by the Cascade Mountains, and southward far into Oregon. The northern and eastern edges of the Plateau where the lava advanced upon the mountains are very sinuous, the summits of some of the higher marginal foothills being completely surrounded by lava.

The aggregate of these basalt layers (the "Columbia River basalt") covered the older erosional surface to a depth of over 1,000 meters in places. The increasing weight thus brought to bear upon the older surface caused it to subside, bringing the upper surface of the basalt down to about 200 meters above sea level in the middle of the Plateau.

Early in the Pliocene when the lava flows had practically ceased, the Cascade Mountains, which previously had had slight relief, uplifted considerably. At the end of the Pliocene they were again elevated, this time to an average height of about 2,000 meters. Although the western slope of the shallow lava basin was uplifted to mountainous heights during the Pliocene, the opposite slope remained intact as a plain which sloped gently (about four meters to the kilometer) downward toward the Cascades. In this manner the northern portion of the Columbia Pla-

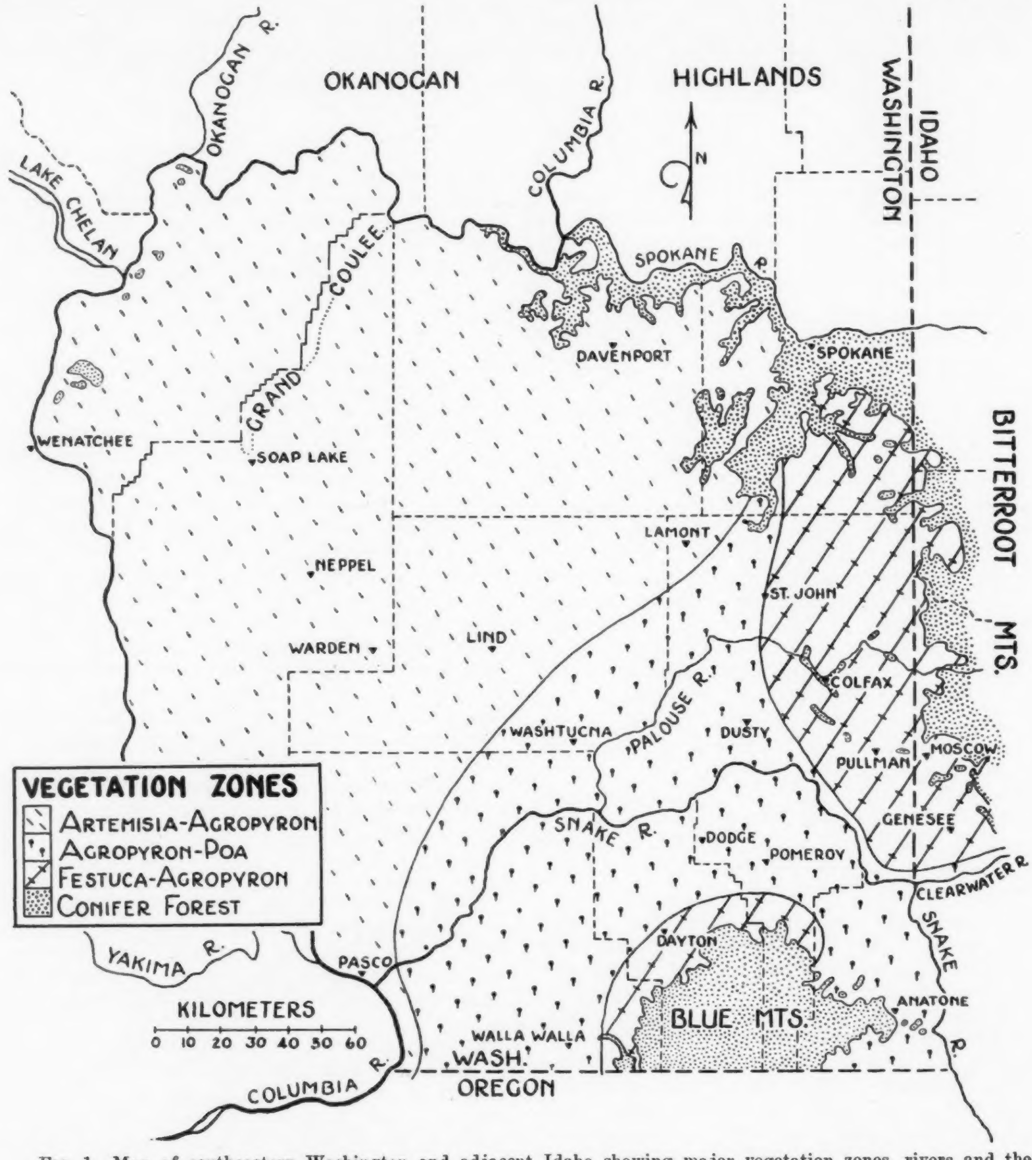

FIG. 1. Map of southeastern Washington and adjacent Idaho showing major vegetation zones, rivers and the principal towns.

teau came to be surrounded on the third side by mountains.

Subsequent folding took place in local parts of the remaining plain, the most noteworthy effect of which was the formation of the Blue Mountains which extend southward from the southern border of Washington. These are not quite extensive enough in an east-west direction completely to cut off the northern portion, that is the Walla Walla section, of the Columbia Plateau from the more extensive southern portion.

With the elevation of the Cascades in the Pliocene epoch, the climate of southeastern Washington became very arid due to the interception of the moist westerlies by the mountains. Fossil floras contained in the thin layers of lacustrine deposits which are interbedded between the basalt layers show that during the period of lava extrusions and prior to the appearance of the wind-barrier to the west, the area had a temperate oceanic climate. As late as the upper Miocene the region supported a luxuriant forest containing Acer, Ulmus, Tilia, Carya, Quercus, Lirioden-

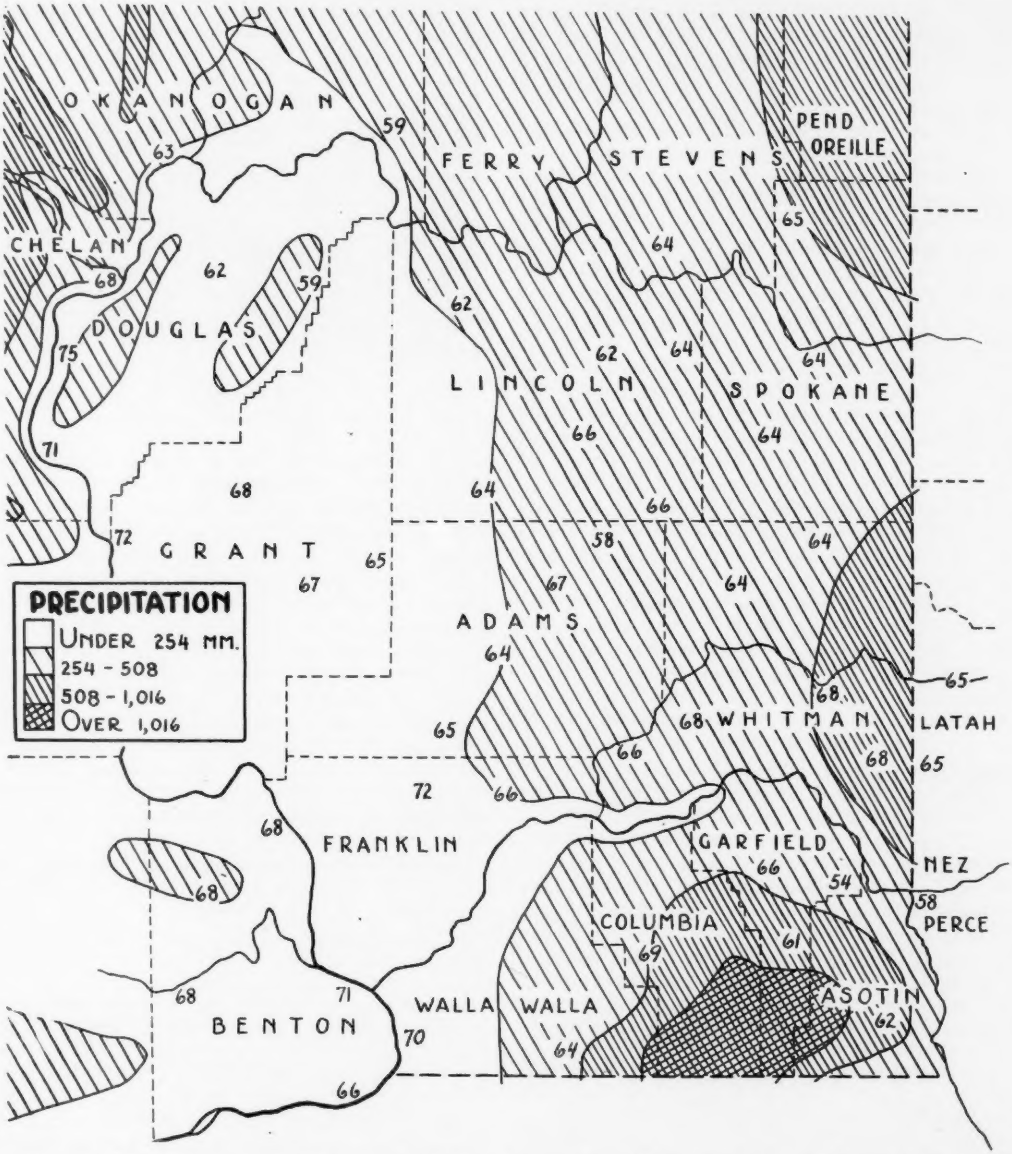

FIG. 2. Map of southeastern Washington showing the counties, and some isohyets of annual precipitation (after a map by the Washington Agricultural Experiment Station, Pullman, Washington). The scattered figures give the percent of the annual precipitation which falls at those points during the six winter months of October through March.

dron, Magnolia, Taxodium, Sequoia, Ginkgo, Pinus, Ficus, Sapindus, and Laurus (Berry, 1929).

As the forests disappeared in Pliocene time, desert and grassland species began to migrate into the basin from the south and east where older arid regions had fostered their development. By early Pleistocene time the trend toward a desert climate had culminated in a long dry period during which the soil was not thoroughly stabilized by a complete vegetational cover.[1] The mantle of silty residual material which had been produced by the rapidly decomposing basalt was at this time blown by southwest winds into dune-like hills which today are about 50 meters high where they occur along the eastern edge of the Plateau. Most of the residual material thus became essentially loessal in character. In places this silty

[1] The occurrence of elephant and horse bones in the loess bears out the assumption of a dry climate, and also indicates the age of the loess (Bryan, 1927).

blanket attains a thickness of nearly 100 meters. It is a rich agricultural soil, and is so porous and well aerated that earthworms and the roots of certain plants sometimes are found over 3 meters below the surface (Weaver, 1915).

The occurrence of layers of loess of different ages, colors and thicknesses indicates that the mass is the product of several distinct periods of eolian activity (Bryan, 1927). Furthermore, this prehistoric period of soil-blowing must have been of mild intensity and long duration; otherwise the depressions in the undulating topography would not have maintained such perfect drainage under the arid climate, nor would the loessal blanket have retained much thickness in the southwest portion of the Plateau.

The principal stream in this region is the Columbia River. The course of this river as well as that of its principal tributaries, the Spokane and Snake Rivers, may be seen in Figure 1. The water of all the rivers is derived from mountainous regions at varying distances from the Plateau. Streams arising in the Plateau are strictly intermittent. In general, they flow away from the center of the Plateau toward the Columbia or one of its major tributaries.

The soil materials over much of the Plateau were greatly affected by Pleistocene glaciation. During a pre-Wisconsin ("Spokane") advance upon the region, the ice pushed southward through the five wide north-south valleys of the Okanogan Highlands but extended only slightly onto the Plateau. In northern Douglas County the edge of this ice sheet blocked the channel of the Columbia River as it flowed westward along the southern border of the highlands, so that the voluminous drainage waters from the melting ice were forced to seek new channels southwestward across the hills of the loessal Plateau (Bretz, 1923). Flowing off the ice front all along the north edge of the Plateau, the melt waters formed a braided system of broad drainage channels, extending in a southerly and westerly direction to the Snake and lower Columbia Valleys. The loessal material was quickly stripped from the paths of these prodigious streams (Fig. 3), and the swift, turbid waters, sometimes over 100 meters in depth (Bretz, 1923), scoured deeply into the basalt. Along the main lines of drainage great steep-walled troughs were cut into the vertically jointed rock (Fig. 4).

FIG. 3. Outcropping of basalt in scabland strip south of Lamont, Washington. Loessal hills in background.

FIG. 4. Canyon of the Palouse River which was excavated down the center of a broad Pleistocene drainage course. Note the distinct layers of basalt.

With the final wasting of this glacier, the old channel of the Columbia River became divested of its covering of ice so that the melt waters reexcavated it, and since it was much deeper than the temporary channels the waters receded entirely into it. Later, during the Wisconsin glacial stage, the drainage of the Columbia River was again temporarily blocked by a similar advance of ice, and once more the valley overflowed bringing about further erosion of the channels previously established.

These glacial episodes obviously had a great influence upon the soil materials of the Plateau. In the lower, western portion of the Plateau scarcely half of the original area of the loessal blanket remained. This area which was so profoundly altered by glaciofluvial activity includes all of the area designated as Artemisia-Agropyron region in Figure 1, and approximately the western half of the Agropyron-Poa region. The only remnants of the old loess in this flooded area exist in the form of isolated island-like mounds elongated in the direction of flow of the melt waters. Their height attests the original depth of the preglacial material. Between these ridges the extensive network of abandoned water courses is marked by 725,200 hectares scoured to the basalt (Fig. 3), and an additional 233,100 hectares left buried by glaciofluvial debris (Bretz, 1923). The term "scablands" is locally and appropriately applied to the areas denuded down to the basalt, and the deep canyons which were cut into the rock surface of the scabland strips are known as "coulees."

Grand Coulee, the most famous of the latter, extends in a southwesterly direction away from the Columbia Valley (Fig. 1). This channel varies from 1.5 to 8.0 kilometers in width and attains a depth of about 300 meters. Where it leaves the Columbia Valley it hangs approximately 194 meters above the present stream.

Since the recession of the last glacial floods from the scablands, there has been relatively little soil-blowing except for a slow continual transfer of material from windward to leeward slopes. Bryan (1927) reports that Pleistocene drift in the vicinity

of Spokane bears a mantle of loess, probably tufaceous (Waters and Flagler, 1929), varying from 4 to 9 decimeters in thickness. Likewise the glacio-fluvial deposits observed by the writer throughout the region of study are characteristically covered with a layer of postglacial loess of similar thickness. These facts point to the conclusion that there has been relatively little soil-blowing in the region during the post-Pleistocene interval of about 30,000 years, and that this interval on the whole has been more humid than the period immediately preceding glaciation when most of the wind action took place. Dust storms were practically unknown to the early settlers of this region. However, the agricultural development which has taken place, particularly the ill-advised attempts to cultivate parts of the most arid regions, have been accompanied by a steady increase in the number of dust storms (Bryan, 1927), although they have not yet approximated the severity of those of the Great Plains area. A few recent measurements of dust deposition along the eastern edge of the Palouse region indicate daily falls ranging up to 67 grams per square meter, with an annual sum of 237 grams (Peterson, 1922).

Our knowledge of the modern vegetation of this northern segment of the Columbia Plateau begins with post-Pleistocene time. Studies of the stratification of pollen fossils in peat which has accumulated since the last glaciation indicate that immediately following the Wisconsin period of the Pleistocene the vegetation, at least in the vicinity of Spokane (Hansen, 1939), was very similar to that of today. The xerothermic period which intervened between the beginning of post-Pleistocene time and the present caused a temporary extension of the limits of the prairie and desert zones which for a time encroached upon the receding forest edge and then returned to resume their former positions.

CLIMATIC CHARACTERISTICS

PRECIPITATION, SOIL MOISTURE, AND RUNOFF

The rain-shadow effect of the Cascade Mountains is most pronounced along the western, lower edge of the Plateau. As shown in Figure 2, the total annual precipitation is relatively low here, and increases gradually up the slope eastward toward the forested semicircle of mountains.

An unfavorable precipitation/evaporation ratio unquestionably prevents the attainment of forest vegetation on the Plateau. Likewise the seasonal distribution of precipitation has been a critical factor through the selective influence it has exerted upon the immigration of species onto this unforested plain. Generally between 65 and 70 percent of the total annual precipitation falls in the six winter months of October to March inclusive (Fig. 2). Not only is the ratio of winter to summer precipitation high, but the actual number of days in winter with 0.25 mm. or more of precipitation is rather high for this latitude and distance from the sea (Kincer, 1922).

As a result of this uneven distribution of precipitation, growth water is available in the upper soil layers only during and immediately following the rainy winter season. Weaver's studies (1917) at Pullman, Washington, showed that the autumn rains which at this edge of the Plateau begin about the end of September fall on a soil which is lacking in growth water to a depth of about 6 to 9 decimeters. During the ensuing winter, precipitation falling either as slow gentle rains or as wet snows of relatively short duration soaks into the loess and gradually saturates the surface layers. The thickness of this saturated zone increases progressively, its lower limit reaching a depth of about 2 decimeters in October, and about 12 decimeters by March. By the time active growth is resumed in the spring there has accumulated a deep wet surface horizon. This moist layer functions as a reservoir which, during the ensuing months, is gradually exhausted of growth water by plant absorption and by evaporation, to a depth of nearly a meter. Westward, in drier portions of the area, there occurs a similar sequence, but involving less moisture, so that the more limited supply of growth water there is exhausted earlier in the summer (Table 5).

Runoff in the primeval state was almost nil (Rockie, 1939), although the steepness of most of the loessal slopes is between 20 and 40 percent, with steeper ones quite common. Rounded troughs lacking evident stream courses originally separated the loessal hills. After cultivation has reduced the porosity of the upper horizons, erosion develops to serious though often inconspicuous proportions in these loessal soils.

Rockie (1939) also cites the statement of an old Amerind that in this region "channels now dry except during the flood season were occupied by small but permanent streams, in which trout could be caught at any time." Although this may well have been true for a narrow zone near the mountains, there is strong ecological evidence that permanent streams were exceptionally rare under primeval conditions. In the first place, one of the main obstacles met by the cattle industry which began when southeastern Washington was first settled by white men was the lack of water for livestock (Strahorn *et al.*, 1929). Further evidence of the same type is the fact that the large ungulates which populated the grasslands to the east of the Rocky Mountains were absent or rare in southeastern Washington. Lewis and Clark observed in 1806 that "there is, in fact, very little difference in the face of the country here from that of the plains on the Missouri (River), except that the latter are enlivened by vast herds of buffalo, elk, and other animals. . . ." (Hosmer, 1903, p. 279). This same source reveals elsewhere that there were a few antelope in the Palouse region, but the deer and elk were practically confined to timbered areas, which in all probability had small, permanent streams where the animals could water. Records of explorers in 1812 (Irving, p. 280) and trappers in 1824 (Van Osdel, 1915, pp. 166-167) substantiate these obser-

vations of Lewis and Clark as to the confinement of deer and elk to the forested foothills. An 1811 account specifically mentions that travel was necessarily restricted to the major stream courses to insure water and meat (consisting of fish and beaver) for the travelers (Irving, p. 220). All of these data strongly indicate that the low rainfall and high absorptive qualities of the virgin soils resulted in a paucity of permanent streams so that in its primeval condition the region under study was essentially inimical to the existence of all the characteristic ungulates of North America, except for the hardy antelope.

Temperature

Summer temperatures are about as hot as might be expected in an inland region at such low elevation, but winter temperatures are decidedly high considering the latitude and distance from the sea. The relative mildness of the winters is evidenced by isotherms of average minimal temperature for the year, and of average monthly temperatures of fall, winter, and spring (Kincer, 1928). The average diurnal range of temperature is relatively low in winter.

Evaporation, Cloud, and Fog

Summer evaporation in southeastern Washington is rather high in relation to the amount of precipitation received during this season. In fact, the precipitation/evaporation ratio for June, July, and August is as adverse in southeastern Washington as in the true deserts to the south, and is considerably less favorable than in the prairies east of the Rocky Mountains (Livingston and Shreve, 1921, p. 337). A summary of data from all the U. S. Weather Bureau evaporation instruments maintained in the region of study is contained in Table 1.

TABLE 1. Precipitation/evaporation ratios for six summer months at the three evaporation stations which have been established in the region of study. All existing records of precipitation and evaporation were used in these calculations regardless of the differences in the number of years of record of any type of data.

U. S. Weather Bureau Station	Zone	Apr.	May	June	July	Aug.	Sep.
Lind, Washington...	Artemisia-Agropyron......	0.13	0.15	0.10	0.02	0.04	0.10
Walla Walla, Washington...	Agropyron-Poa............	0.31	0.18	0.13	0.02	0.05	0.18
Moscow, Idaho........	Festuca-Agropyron......	0.52	0.37	0.22	0.08	0.10	0.29

Winters in southeastern Washington are so cloudy and foggy that only about 25 percent of the total possible sunshine reaches the ground during that season (Kincer, 1928). In fact, this influence is so pronounced that the mean relative humidity for the entire year is rather high as compared to adjacent regions to the south and east.

VEGETATION ZONES

The essentially unforested area considered in this study may be divided into three zones (Fig. 1) each of which is characterized by a distinct climatic climax association. In addition to the latter, each zone embraces edaphic, biotic, and fire climaxes[2] as well as seral associations. Only those associations which cover considerable area in the aggregate have been considered.

The three climatic climax associations, listed from the most xerophytic to the most mesophytic, are (1) the *Artemisia tridentata-Agropyron spicatum*[3] association, (2) the *Agropyron spicatum-Poa secunda* association, and (3) the *Festuca idahoensis-Agropyron spicatum* association. For the sake of brevity these will subsequently be referred to as the Artemisietum, the Agropyronetum, and the Festucetum.

Within the timbered foothills (Fig. 1) the forest zones, based on climatic climaxes and listed in order of increasing elevation, are: (4) *Pinus ponderosa* zone, (5) *Pseudotsuga taxifolia* zone, (6) *Thuja plicata-Tsuga heterophylla* zone, and (7) the *Picea engelmannii-Abies lasiocarpa* zone.

A map of vegetation zones (Fig. 1) was made in the field during excursions into all sections of the shaded area. In the aggregate several thousand kilometers of highways and side roads were traveled to locate virgin and near-virgin relics, and to determine the extent and variation in structure of the associations under study. In spite of the great amount of effort expended in search of relic stands of original vegetation, too great reliance cannot be placed upon the exactness of the boundary lines on the map. It proved difficult in some places to find sufficient relics to judge the nature of the original vegetation. Also there was the inevitable problem of drawing a line where in the field a transition is encountered. In places the lines, which are intended to pass through the middle of ecotones, may err as much as 10 kilometers, but for the most part the writer believes the errors to be of less magnitude.

The fundamental value of the climatic climax as a basis for classification of edapho-vegetational provinces, at least in this region, is attested by the close correlation between such vegetational zones and major soil divisions. After the vegetational zones had been delimited entirely from field observations, it was discovered by examination of soil survey maps that there exists a close correspondence between the following:

[2] To avoid possible misunderstandings, these terms are used in this paper according to the following definitions. A *climatic climax* is an apparently permanent association the development of which has been conditioned only by the limitations of the existing climate and flora, which are factors influencing the composition of every plant association. An *edaphic climax* is an apparently permanent association in which a third factor, substratal peculiarities, exerts a strong limiting influence upon the community in addition to those imposed by climate and flora. In a similar manner, *biotic*, *fire*, and *topographic climaxes* may be recognized and designated on the basis of a third major determining factor.

[3] Throughout this paper the name *A. spicatum* (Pursh) Scribn. & Smith will be used to include this species and the very closely related *A. inerme* (Scribn. & Smith) Rydb. with which it merges completely. As indicated previously (Daubenmire, 1939) the two possess similar and unique physiological traits and, except for the intergrading awn character, cannot be distinguished morphologically, so that the significance of a rigid distinction in an ecological study in no way merits the great amount of time and labor which such a practice would entail.

the Artemisia-Agropyron zone and the Wheeler soil series
the Agropyron-Poa zone and the Ritzville soil series
the Festuca-Agropyron zone and the Palouse soil series.

There is relatively little correlation between other types of climaxes and particular soil divisions as recognized in the existing soil surveys.

THE ARTEMISIA-AGROPYRON ZONE

THE ARTEMISIETUM

Within the area designated in Figure 1 as the Artemisia-Agropyron zone, the climax association of the loamy uplands was dominated under primeval conditions by *Artemisia tridentata* Nutt. and grasses among which *Agropyron spicatum* was conspicuous. The former is a deep-rooted evergreen shrub, and the latter a tall perennial grass.

Only two essentially virgin areas of Agropyronetum were discovered in Washington, neither of which is particularly representative of the main body of the association since both are located near the eastern (mesic) extremity of the zone.

One of these is the unused portion of a rural cemetery situated a few kilometers southeast of Lamont, Washington. This area seems to have been completely protected against any kind of disturbance since 1889. Furthermore, the completeness with which the vegetation has become reestablished upon the oldest graves demonstrates that ample time has elapsed since 1889 for a complete recovery from the effects of any disturbance to which the vegetation might previously have been subjected. This tract is on a gently sloping loessal hill and faces ESE. The excellence of the soil here is attested by the closeness with which all the surrounding land is utilized for wheat production.

Three types of vegetation are included within the cemetery. The lower edge of the tract includes a small portion of the flat valley bottom, which supports a stand of Elymus. Around the edge of the Elymus stand, on the lowest portion of the slope, occurs a relatively mesic phase of the Artemisietum. In this zone *Festuca idahoensis* and *Stipa columbiana*[4] are the dominant grasses accompanying the sagebrush, and in addition there is a conspicuous proportion of forbs such as *Lupinus sericeus, Lithospermum ruderale, Geranium viscosissimum, Calochortus macrocarpus,* and Potentilla. On the highest part of the slope which is included within the fence, the forbs and Stipa are very scarce, and Agropyron assumes more importance, although Festuca remains the dominant grass.

On June 5 a plot 1 x 10 meters was laid out in a representative portion of this upper part of the cemetery, and all the grasses and forbs which were fully developed at that time were clipped to the ground line. The results, expressed as weight of oven-dry material per 100 square meters, are:

Festuca idahoensis	8,360 g.
Agropyron spicatum	1,094
Astragalus spaldingii	628
Balsamorhiza sagittata	614
Carex filifolia	609
Lupinus sericeus	46

In addition, the plot contained still smaller amounts of *Poa secunda, Phlox longifolia, Stellaria nitens,* and *Bromus tectorum*.[5] Artemisia, which was not clipped, covered 2.2 percent of the area by the vertical projection of its foliage.

The amount of Festuca in this stand is considerably higher than in the majority of near-virgin stands of the Artemisietum which the writer has examined in south-central Washington and adjacent parts of Oregon. It is possible that this grass was originally just as abundant over most of the area but was nearly eliminated from the unprotected stands because of its very high palatability to livestock. On the other hand, its relative abundance at Lamont may well be due to the location of the stand at the lower portion of a favorably exposed slope, and near the mesic eastern limit of the Artemisia-Agropyron zone (elevation 610 meters). Furthermore, the increase in importance of Agropyron near the top of the slope strongly suggests that the tract as a whole is more mesic than the hilltops. From a synthesis of notes taken on numerous and extended surveys it appears that Agropyron was usually the most important herb in the virgin Artemisietum of Washington.

The second of the practically virgin stands of Artemisietum which the writer discovered is located in a cemetery 13 kilometers ENE of Davenport, Washington. The moisture balance is very high here, for the edge of the forest is but a few kilometers distant, and the stand is even less reliable as an indicator of the typical, primeval Artemisietum such as existed near the center of the Artemisia-Agropyron zone. In this cemetery small sagebrush plants grow interspersed in a dense stand of grasses (*Agropyron spicatum, Festuca idahoensis, Stipa columbiana*) and perennial forbs (*Balsamorhiza sagittata, Lupinus sericeus, Hieraceum albertinum, Lithospermum ruderale, Castilleja lutescens, Erigeron corymbosus*). Save for the presence of the sagebrush, this piece of vegetation is strikingly similar to the Festucetum which borders the forest farther south.

There appear to have been three minor types of variation in the shrubby element of the Artemisietum throughout central Washington. In places *Salvia carnosa* Dougl., a shrub similar to *Artemisia tridentata* in appearance and ecology, grows intermingled with the latter. Wherever the soil varies toward sandiness, Chrysothamnus (especially *C. nauseosus* (Pall.) Brit.) is commonly present in the association, and where the soil is shallow and stony *Artemisia rigida* (Nutt.) Gray appears.

This Artemisia-Agropyron zone in Washington has been variously referred to as "desert," "semidesert,"

[4] The authorities for species listed in Tables 2 and 6 will not be repeated elsewhere in the text.

[5] The role of exotic species in native communities is discussed later.

and "grassland." The low rainfall (as low as 16.4 centimeters at Wapato, Washington) and high temperatures, plus the omnipresence of shrubs, give the region some important characteristics of a true desert. On the other hand, the closed nature of the plant cover, and the dominance of grasses in the community, link this association closely with the grassland formation. Perhaps the designation of semidesert is most appropriate.

THE BIOTIC CLIMAX

Little remains of the previously extensive Artemisietum in Washington. By alternate years of fallowing and cropping, fair though not too dependable crops of wheat are obtained on the loessal soils in the northern and eastern portions of the zone. Between cultivation on the one hand, and heavy grazing and fire on the other, the climatic climax has been reduced to scattered stands, most of which give little suggestion of the original luxuriance of the type.

FIG. 5. An undisturbed stand of the Artemisietum in a rural cemetery south of Lamont, Washington. Photographed in September when grasses are dormant and sagebrush is in fruit. The stake which appears in this and in subsequent photographs is one meter in length and is marked off in decimeter units.

The influence of heavy grazing upon the savanna-like Artemisietum tends to eliminate first the large forbs and grasses, and then the smaller plants, so that under extreme grazing the ground between the shrubs becomes almost barren of vegetation. *Artemisia tridentata* is browsed to a very slight extent, although the less common *A. rigida* is very palatable and is summarily reduced to a compact cushion-like form about a decimeter in height. Under continued grazing and in the absence of fire, there is a tendency toward the development of a biotic climax consisting of a nearly pure stand of *Artemisia tridentata*.

It seems to have been well established in regions to the south and east of Washington (in southern Idaho, Craddock and Forsling, 1939; and in the Great Basin region, Pickford, 1932) that the abundance and size of Artemisia plants increase as livestock graze out the accompanying herbs. This same phenomenon has probably occurred in southeastern Washington as well, but the writer has yet seen no scientifically incontestable evidence in support of such a statement. On the other hand it is quite possible that the dense stands of Artemisia which occur on the Plateau at lower elevations than the two near-virgin areas cited may have originated by an increase in Artemisia following the elimination of the grass synusia. Since there seems to be no question but that sagebrush was a conspicuous member of the flora before the advent of white man,[6] only the discovery of well-preserved relics or a study of exclosures over a long period of years can provide information as to the relative importance of Artemisia in the typical climatic climax.

THE FIRE CLIMAX

Locally, the practice of burning the vegetation, which was started by the aborigines and is continued today, appears to have played a great part in eliminating Artemisia from the Artemisietum, especially in the northern and western parts of the zone. Apparent evidences of this influence are manifold. Often a remnant of the original vegetation on one side of a road (which acts as a fire barrier) contains none of the shrub while a remnant on the other side does. Deeply charred fenceposts often accompany shrubless stands. Frequently there may be encountered stands in which Artemisia is regenerating after a light burn, with a cluster of straight sprouts emerging from a single charred crown. About 1 kilometer northwest of the cemetery where the coverage studies were made there is a fine example of such a condition. The straight crown-sprouts of the few remaining shrubs are strikingly different from the heavy, crooked, and usually single trunks of the shrubs in the protected cemetery (Fig. 6). Apparently Artemisia has the ability to sprout in this manner only in the more mesic eastern portion of the range of the Artemisietum. The higher temperature, lower humidity, and lower moisture content of the litter in the drier parts of the Plateau undoubtedly result

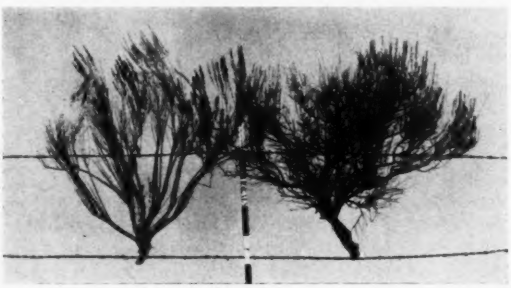

FIG. 6. Two plants of *Artemisia tridentata* severed about three centimeters below the ground line. Plant to the right is a typical specimen from the Lamont cemetery (Figure 5). Plant to the left is from a near-virgin burned area about one kilometer distant. The sprouts were distinct at the 3 cm. level and had to be tied together at the base to be photographed in their natural positions.

[6] An account written by a trapper in 1824 refers to parts of the plateau of the Spokane as a "barren sage plain" (Van Osdel, 1915, p. 160). This and other historical records, as well as studies of cemeteries, point to the conclusion that sagebrush has not entered the region north of the Blue Mountains as a consequence of overgrazing.

in hotter fires there, and possibly this accounts for the higher mortality when sagebrush is burned at the lower elevations.

Another interesting example of the influence of fire is to be found in a cemetery about two kilometers south of Warden, Washington. Today the unused portion of this fenced enclosure supports a handsome stand of Agropyron together with other herbs of the Artemisietum, but sagebrush is absent. Furthermore, there is no trace of Artemisia along the fencerows adjacent to the cemetery. The farmer who lives across the road recalls a great fire which swept the country before the land was broken for cultivation. This fire, he stated, killed practically all the sagebrush so that a short while afterwards when the cemetery was established, there were very few shrubs (probably seedlings) to be grubbed out. In this region, which is considerably west of the Lamont area, Artemisia roots do not send up new shoots after a fire. The persistence of the herbs in the Warden cemetery, as well as in other locations, attests their relative immunity from fire in contrast with Artemisia. The fire climax differs from the Artemisietum chiefly in the absence of Artemisia.

The writer has found that studies of the unused portions of rural cemeteries in this zone are not as fruitful as in the prairie zones, for it is customary to grub out the sagebrush when the cemeteries are established, and often to burn them periodically as well. The only cases discovered where a cemetery in the Artemisietum seems to have escaped such disturbance are the stations near Lamont and Davenport.

Other Plant Associations within the Zone

In addition to the fire and biotic climaxes mentioned previously, there are many edaphic climax types. The most important of these may be classified as follows:

- I. On sandy soils
  1. Chrysothamnus association
  2. Chrysothamnus-Purshia association
  3. Artemisia-Purshia association
  4. Oryzopsis association
  5. Stipa association
- II. On moist or poorly drained soils
  - A. On saline soils
    6. Distichlis association
    7. Sarcobatus-Distichlis association
    8. Grayia association
  - B. On non-saline (or weakly saline) soils
    9. Elymus association
    10. Streamside forests and thickets
- III. On thin soils of basalt outcrops
    11. *Artemisia rigida* association
    12. *Pinus ponderosa* association

CHRYSOTHAMNUS ASSOCIATION

Rabbitbrush, including all varieties and forms of *Chrysothamnus nauseosus* and *C. viscidiflorus* (Hook.) Nutt. found in southeastern Washington, is the most characteristic plant of sandy soils. *Tetradymia canescens* D.C., a shrub very similar in appearance and ecology, often accompanies rabbitbrush. Frequently the soil is not sandy enough to foster a typical Chrysothamnus association, and at the same time is too coarse textured to allow a typical development of the Artemisietum, so that apparently climax mixtures of sagebrush and rabbitbrush are not uncommon. Burning such a mixed association favors the Chrysothamnus which sprouts vigorously from the stumps after all but the hottest fires, whereas Artemisia is much more easily killed out by burning, especially westward.

The nature of the variations in sandy soils which result in the grouping of sand plants into the five associations recognized in this zone is not known. That these differences are not too pronounced is indicated by the great overlapping of species and consequent intergradation of the associations. The Artemisietum may be found on soils as coarse as alluvial gravels, but the writer has never seen it on a sandy soil so lacking in colloidal material as to resemble dune sand. A fine illustration in point occurs just west of Neppel, Washington, where there exists an extremely sharp line between the Artemisietum and the Chrysothamnus-Purshia association which corresponds to a line of contact between two deposits of alluvium, one a sand and the other a sandy loam.

Salsola pestifer A. Nels. occurs as a weed on broken ground throughout central Washington; it invades near-virgin vegetation only in the case of sandy soil communities.

CHRYSOTHAMNUS-PURSHIA ASSOCIATION

Large areas of the dark colored sands west of Neppel, Washington, are dominated by a mixture of rabbitbrush and bitterbrush, *Purshia tridentata* (Pursh) D. C. This is the only region in southeastern Washington where the writer has seen this association.

ARTEMISIA-PURSHIA ASSOCIATION

In certain areas the alluvial sandy loams along the Columbia River and its major tributaries originally supported a mixture of sagebrush and bitterbrush. The outstanding success of irrigated orchards which have been planted in some of these areas is a good indication that similarly vegetated terraces will have equal agricultural value when irrigation water becomes available to them.

ORYZOPSIS ASSOCIATION

Open stands of the bunchgrass *Oryzopsis hymenoides* (Roem. & Schult) Ricker occur on dune and alluvial sands. Despite the open nature of the association, it seems fairly efficient in preventing soil-blowing, so that the grass has value as a sandbinder as well as being good forage.

STIPA ASSOCIATION

Relatively pure stands of *Stipa comata* Trin. & Rupr. are not particularly frequent, although the species is widely distributed. In southeastern Washington it almost invariably indicates a sandy soil.

DISTICHLIS ASSOCIATION

In pronounced alkali basins, *Distichlis stricta* (Torr.) Rydb. dominates a zone immediately about the barren center of the depression (Fig. 7). This grass is also encountered frequently as island-like patches on habitats where salinity is much less severe than in the basins mentioned. The observations on the distribution of Distichlis in Washington indicate that the grass is a good indicator of slight to extreme salinity plus a high water content of the soil during the early growing season.

FIG. 7. Zonation of vegetation around an alkali basin in the floor of the Grand Coulee. Around the barren center is a zone of *Distichlis stricta*. The adjacent fringe of shrubs whose foliage photographed dark is *Sarcobatus vermiculatus*. In the distance is the gray-green *Artemisia tridentata*. Along the ecotone between the Sarcobatus and Artemisia zones is a poorly defined belt of *Grayia spinosa* which cannot be distinguished in the picture.

SARCOBATUS-DISTICHLIS ASSOCIATION

Sarcobatus vermiculatus (Hook.) Torr., usually accompanied by an inferior synusia of Distichlis, occurs frequently on saline soils in the Artemisia-Agropyron zone, especially westward. The manner in which the Distichlis synusia extends beyond the shrub synusia to become an association on the lower slopes of an alkali basin probably signifies that the difference between the salt tolerance of these two species is less than their relative abilities to endure a high water table. In other regions the writer has observed that Sarcobatus is easily killed by an elevation of the water table which is occasioned by an unusually wet year.

Not only does Distichlis exhibit a wider latitude of habitat tolerance where it occurs in the same region with Sarcobatus, but the grass is more frequently encountered east of the Columbia River than is the shrub.

GRAYIA ASSOCIATION

The Artemisietum is tolerant of very little alkali. Whenever the salt concentration exceeds but slightly the tolerance of the Artemisietum, hopsage (*Grayia spinosa* (Hook.) Moq.) dominates. In the concentric series of vegetational zones about an alkali basin (Fig. 7), Grayia typically occurs between the Artemisia-Agropyron and Sarcobatus-Distichlis associations.

Certain shrubby halophytes which are so abundant in sagebrush regions to the south of the Blue Mountains are either absent (as *Atriplex confertifolia* (Torr.) S. Wats., and *Allenrolfia occidentalis* (S. Wats.) Kuntze.) or relatively uncommon (as *Eurotia lanata* (Pursh) Moq.) in southeastern Washington.

ELYMUS ASSOCIATION

Elymus condensatus Presl. is a species preferring, in our region, a year-around supply of soil moisture such as occurs in clay bottomlands or seepage areas. In the western part of the Artemisia-Agropyron zone the bottomlands are generally dominated by the three halophytic associations mentioned above, but eastward where there is much less alkali, Elymus dominates the corresponding part of the topography.

STREAMSIDE FORESTS AND THICKETS

Species of Populus and Salix form a thin and very discontinuous fringe along the banks of permanent streams, or other habitats where a relatively non-saline water table is near the surface at all times. A similar ecological role is played in this region by *Juniperus scopulorum* Sarg. which is occasionally found on the cobble shores of the Columbia River.

Two species of arborescent Junipers are found in southeastern Washington, although the numbers of specimens of both are very low. *J. scopulorum* extends northward through this region east of the Cascades into British Columbia, occurring on thin rocky soils along the low terraces or bluffs of the Columbia and other rivers at low altitudes. *J. occidentalis* Hook. enters Washington from the south, occurring on dry ridges of the Blue Mountains and rock bluffs of the Columbia Valley as far north as the southern end of Grant County.

ARTEMISIA RIGIDA ASSOCIATION

In the eastern half of the Artemisia-Agropyron zone the thin soils of the scablands frequently support stands of *A. rigida* (Nutt.) Gray. This community is easily recognized from a distance by the aspect of the shrubs, which are so palatable that livestock keep them browsed to a low cushion-like form about a decimeter tall.

PINUS PONDEROSA ASSOCIATION

On the scablands in the northeast extremity of the Artemisia-Agropyron zone strips of pine (*P. ponderosa* Dougl.) savanna or forest extend southward from the Okanogan Highlands (Fig. 1).

THE AGROPYRON-POA ZONE

THE AGROPYRONETUM

Progressively eastward over the loessal uplands of the Plateau the abundance and stature of *Artemisia tridentata* decrease until the climatic climax vegetation is completely lacking in this shrub. Eastward beyond the limits of sagebrush there occurs on the uplands a prairie dominated chiefly by the herbs which

form the characteristic inferior synusiae of the Artemisietum. The appearance, if not the composition, of the vegetation just east of this ecotone is very distinctive. In the absence of Artemisia the bunchy habit of Agropyron becomes very evident, even at a distance (Figs. 8 and 9).

FIG. 8. An area in eastern Franklin County which has been protected from grazing since 1911. On the hill slope is a stand of Agropyronetum. On the sandy alluvium in the ravine bottom in the foreground is an edaphic climax of Chrysothamnus. Scabland topography in the distance.

FIG. 9. The Agropyron-Poa association in Franklin County, Washington. Picture was taken on April 25 when the tiny interstitial plants were at the height of their development, but before the new foliage of Agropyron had emerged through the bleached shoots of the previous year. Soil moisture studies were made at this station.

The Agropyron plants, which in this association are strictly without horizontal rhizomes, retain their characteristic appearance the year around. Each year new leaves come up through a dense tuft of erect dead shoots which represents the accumulation of several years, and the inflorescences likewise remain erect long after the spikelets drop.

There are about 480 to 500 bunches of Agropyron per 100 square meters of area. The ground between these large bunches (Fig. 9) is fairly well covered with small plants, mostly annuals, which are evident only during the spring. In this lesser vegetation *Poa secunda*, a small bunchgrass, is the most important perennial.

The chief variation in the structure of this climatic climax within the Palouse region is an infusion of large forbs (*Balsamorhiza sagittata, Lupinus sericeus, Potentilla blaschkeana, Sieversia ciliata, Geranium viscosissimum,* and *Hieracium albertinum*) in the community in a narrow strip along the eastern and northern borders of the zone. Although these forbs are more characteristic of the Festucetum, their presence here does not take away from the three most diagnostic characters of the Agropyronetum: the strictly bunch habit of Agropyron, the overwhelming dominance of perennial grasses over forbs, and the presence of *Poa secunda* in the community.

CONSTANCY

As used in this paper, constancy may be defined as the number of occurrences of a species in a series of stands of uniform size, located at widely separated points over the range of the association. Only six near-virgin stands of the Agropyronetum were located during the course of this study. In each of these one or more plots[7] were staked out to obtain constancy data. These plots were 1 x 10 meters each, and were visited at different seasons to obtain complete lists of the vascular plants in each. The stands were distributed among Franklin, Whitman, and Garfield Counties, Washington. The elevation of the lowest is 288 meters and of the highest 440 meters above mean sea level.

Only six out of the 35 species encountered occurred in all 14 constancy plots (Table 2). These may be

TABLE 2. Constancy of vascular plants in 14 stands of the Agropyronetum. Species with the same constancy and in the same synusia are listed alphabetically.

TALL HERB SYNUSIA	
Agropyron spicatum (Pursh) Scribn. & Smith	14
Epilobium paniculatum Nutt.**	11
Festuca idahoensis Elmer	8
Achillea lanulosa Nutt.	7
Calochortus macrocarpus Dougl.	6
Lomatium triternatum (Pursh) C. & R.	3
Sisymbrium altissimum L.	3
INTERMEDIATE HERB SYNUSIA	
Bromus tectorum L.	14
Poa secunda Presl.	14
Brodiaea douglasii Wats.	8
Lupinus sericeus Pursh	3
Erigeron corymbosus (H. & A.) T. & G.	2
Amsinckia retrorsa Suksd.	1
Bromus mollis L.	1
LOW HERB* SYNUSIA	
Draba verna L.	14
Festuca pacifica Piper	14
Lithophragma bulbifera Rydb.	14
Plantago purshii R. & S.	13
Stellaria nitens Nutt.	13
Agoseris heterophylla (Nutt.) Greene	11
Lactuca sp.***	9
Erodium cicutarium (L.) L'Her.	8
Lomatium macrocarpum (H. & A.) C. & R.	7
Madia exigua (Sm.) Gray	7
Agoseris glauca (Pursh) Steud.	6
Astragalus spaldingii Gray	6
Plagiobothrys tenellus (Nutt.) Gray	6
Sisymbrium longipedicellatum Fourn.	6
Claytonia parviflora Dougl.	4
Phlox linearifolia (Hook.) Gray	4
Alchemilla occidentalis Nutt.	2
Cryptantha flaccida (Dougl.) Greene	2
Allium sp.	1
Antennaria dimorpha (Nutt.) T. & G.	1
Lappula redowskii (Hornem.) Greene	1
Total species:	35

*One species, Phlox, suffrutescent.
**In immature condition the writer has been unable to distinguish between this species and *Gayophytum ramosissimum* T. & G. Both species seem to be present but most of the individuals succumb before flowering. All specimens have therefore been lumped under the species which seems most abundant.
***Identity uncertain since the plants were never found in flower in the virgin prairie.

[7] In the most extensive stands, several constancy plots were established in order to obtain enough data of this kind for comparison with the Festucetum, where the more usual procedure was followed, that is, locating each constancy plot in a different stand.

considered the characteristic species of the climax association.

SYNUSIAE

The species in Table 2 are grouped according to similarities in height and general life form. There may be distinguished five synusiae above the ground line:

1. lichen-moss synusia
2. low herb synusia (mostly under 15 cm. in height)
3. intermediate herb synusia (about 20-25 cm. in height)
4. tall herb synusia (about 30-70 cm. in height)
5. endophyllous fungal synusia.

The synusia of crustose lichens and low growing mosses covers the otherwise unoccupied ground rather completely. These plants remain dried and inconspicuous except during the rainy season, from late fall to early spring.

The low herb synusia is rich floristically, and consists largely of annual species; neither of these characters applies to the other phanerogamic synusiae.

Fungi parasitic upon the shoots are not nearly as abundant in this association as in the more mesophytic Festucetum. Leaves of Brodiaea are frequently rusted, *Puccinia calochorti* Peck parasitizes the leaves of Calochortus, and the spikelets of Bromus are usually heavily infested with *Ustilago bullata* Berk.

FREQUENCY

The two best near-virgin stands discovered are located one in eastern Franklin County, and the other in northern Garfield County, Washington. In each stand a series of 100 plots was staked out and visited at intervals during the growing season to determine the frequency of all the vascular species (Table 3). The Garfield station is near the mesic eastern edge of the Agropyron-Poa belt, while the Franklin County station is near the western xeric edge. This difference in position is reflected in the more complete coverage of *Agropyron spicatum* plus *Festuca idahoensis,* and in the richer flora of annual species in the easternmost series. There were 16 species of annuals in the latter as compared to twelve in the former.

DOMINANCE

Measurements of dominance were made at the Franklin County station by comparing species as to the dry weight of the shoot material produced each season per 100 square meters. To obtain these data each species was clipped while it was in the flowering or young fruiting stage. This procedure necessitated clippings at different seasons, and at each season a different but adjacent plot was used. Had all the clippings been made on any one date, some species would have been poorly represented due to their overmaturity and others due to their immaturity.

Those species in Table 2 for which no dominance data are given in Table 4 are those which were either absent from the Franklin County stand, or were present in too small amounts to merit attention. The total weight of this material which was not considered is believed to be less than 1 percent of the total produced by the stand.

TABLE 3. Frequency of vascular plants in two near-virgin stands of the Agropyronetum in Washington. At each station 100 plots, 2 x 5 decimeters each, were arranged in rows with the plots separated by 1 meter.

Species	Franklin County	Garfield County	Mean
Draba verna	100%	98%	99.0%
Poa secunda	99	97	98.0
Stellaria nitens	*	97	....
Bromus tectorum	100	68	81.5
Festuca pacifica	63	99	81.0
Agropyron spicatum	70	90	80.0
Plantago purshii	84	69	76.5
Epilobium paniculatum	58	0**	29.0
Brodiaea douglasii	21	34	27.5
Lithophragma bulbifera	25	*	....
Madia exigua	0**	27	13.5
Festuca idahoensis	0	27	13.5
Plagiobothrys tenellus	12	12	12.0
Phlox linearifolia	0	24	12.0
Agoseris heterophylla	16	3	9.5
Sisymbrium longipedicellatum	1	18	9.5
Lactuca sp.	0**	17	8.5
Erodium cicutarium	1	15	8.0
Achillea lanulosa	6	9	7.5
Claytonia parviflora	0	15	7.5
Gilia gracilis	1	11	6.0
Astragalus spaldingii	2	7	4.5
Aligera grayi Suksd.	0	6	3.0
Calochortus macrocarpus	4	0	2.0
Lomatium macrocarpum	3	0	1.5
Agoseris glauca	1	1	1.0
Lappula redowskii	1	0	0.5
Lagophylla ramosissima	1	0	0.5
Sisymbrium altissimum	0	1	0.5
Total Species:	21	23	

*Present in the plots but not studied.
**Present in the stand, but happened not to be included in the plots.

These data show that (1) perennials dominate over annuals: 9,437 to 461 grams, or 95 percent to 5 percent, and (2) grasses dominate over forbs: 9,646 to 252 grams, or 97 percent to 3 percent. Obviously one perennial grass, Agropyron, is vastly more important from the standpoint of dominance than all the other plants. Viewed from a distance the association seems to be composed entirely of this one species, and when the inflorescences are well developed, the appearance is somewhat similar to that of a field of grain.

Although *Festuca idahoensis* has a constancy of 8/14, it is very poorly represented in the stand where the dominance studies were made. At another near-virgin stand about 11 kilometers east of Hooper, Washington, where this grass is especially well represented in the association, Agropyron shoots weighed 6,786 grams and Festuca shoots 248 grams per 100 square meters.

PERIODICITY

At each visitation of the Franklin County station during the 3 years, phenological notes were taken for each species.

Two major facts were brought out by this study. Firstly, the dry summer is accompanied by a longer season of vegetational dormancy than is the cold winter. From late July until about October when the autumn rains begin the vegetation is uniformly brown and dry, but with the return of moisture the grasses and a few forbs produce small green shoots which usually endure all winter. Secondly, both the vegetative and flowering activities of most of the smaller plants are condensed into a brief spring season (April and May) before the soil moisture is depleted down to the depth of their shallow root systems. It is probably significant that the deeper rooted plants such as Agropyron, Calochortus, and Epilobium flower at a later date (late May and early June). The phenology of the last-named plant seems determined primarily by environment. During summers when there is more moisture than usual, this plant remains green and produces flowers until autumn, whereas the aestivation of all other members of the association seems primarily determined by heredity.

A very striking feature of the phenology results from the fact that each species among the dwarf annuals attains its maximum development at a slightly different date from the others. This brings about a rapidly progressing seasonal sequence in which one species, as it withers, is replaced by another which in turn retains dominance for only a few days. This characteristic of the annual flora makes it very necessary to time one's visits to permanent plots very carefully if all species are to be observed in one growing season.

Some conception of the denseness of each of these successive ephemeral coverings may be conveyed by the following statistics. A single plot 1 decimeter square was found to contain 168 plants of Draba. A meter square plot contained 119 plants of *Festuca pacifica* and 489 plants of *Bromus tectorum*. These figures are undoubtedly higher than average densities, but were in all cases taken from practically virgin prairie.

LIFE FORMS

The life form data as presented in Table 4 show that out of the 27 species considered, 14 are therophytes,[8] 8 are geophytes, 4 are hemicryptophytes, and 1 is a chamaephyte. The abundance of therophytes reflects an environment ecologically similar to true deserts where, during the rainy season, annuals with a rapid growth rate are able to germinate and set viable seed which will carry the species over another prolonged period of dormancy. Geophytes are especially well represented in this flora.

LEAF SIZE CLASSES

Most of the leaves in this association are of the linear, grass-like form. The remainder are either leptophylls[9] or are divided into leaflets which are equally as small. In this respect the Agropyronetum is very distinct from the Festucetum, as will be brought out later.

TABLE 4. Some sociologic characteristics of the species of the Agropyronetum, omitting those whose constancy is less than three (see Table 2).

Species	Constancy	Life Form	Leaf Size	Vitality Class	Dominance*
Achillea lanulosa	7	hemicryptophyte	leptophyll	4	12g
Agoseris glauca	6	geophyte	microphyll	4	3
Agoseris heterophylla	11	therophyte	nanophyll	4	2
Agropyron spicatum	14	hemicryptophyte	nanophyll	4	8,794
Astragalus spaldingii	6	hemicryptophyte	leptophyll	4	75
Brodiaea douglasii	8	geophyte	nanophyll	3	115
Bromus tectorum	14	therophyte	nanophyll	4	411
Calochortus macrocarpus	6	geophyte	microphyll	3	3
Claytonia parviflora	4	therophyte	leptophyll	4	0
Draba verna	14	therophyte	leptophyll	4	**+
Erodium cicutarium	8	therophyte	leptophyll	4	7
Festuca idahoensis	8	hemicryptophyte	nanophyll	4	0
Festuca pacifica	14	therophyte	leptophyll	4	7
Epilobium paniculatum	11	therophyte	nanophyll	3	+
Lactuca sp.	9	therophyte	nanophyll	1	+
Lithophragma bulbifera	14	geophyte	leptophyll	3	....
Lomatium macrocarpum	7	geophyte	leptophyll	1	3
Lomatium triternatum	3	geophyte	nanophyll	4	1
Lupinus sericeus	3	geophyte	microphyll	4	0
Madia exigua	7	therophyte	leptophyll	4	+
Phlox linearifolia	7	chamaephyte	leptophyll	4	0
Plagiobothrys tenellus	6	therophyte	nanophyll	4	16
Plantago purshii	13	therophyte	leptophyll	4	11
Poa secunda	14	geophyte	nanophyll	4	434
Sisymbrium altissimum	3	therophyte	nanophyll	4	0
Sisymbrium longipedicellatum	6	therophyte	leptophyll	4	4
Stellaria nitens	13	therophyte	leptophyll	4	....
Totals: 27 spp.	....	....	....	....	9,898g

*Oven-dry weight of the total shoots clipped close to the ground, per $100m^2$.
**Weight determined, but amounting to 0.5 g or less per $100m^2$.

VITALITY

Within any climax plant community, competition is always an important factor in maintaining the proportions of the different species which compose the assemblage. By means of disseminules and propagules, species of other communities are constantly being introduced into any climax community, but these immigrants are for the most part unable to germinate, or if they can, they are unable to complete their life cycles in the climax association.

The division between climax species which maintain their status and the immigrants which perish is not always sharp. Lactuca, an annual, germinates and grows for a few weeks in the Agropyronetum and then dies, depending each year upon seed from an

[8] Raunkiaer's life form groups (1934) are followed in this paper. Brief definitions are as follows: THEROPHYTES = annual herbs, GEOPHYTES = perennial herbs with perennating buds below the soil surface, HEMICRYPTOPHYTES = perennial herbs with buds at the ground line, CHAMAEPHYTES = suffrutescent herbs or low shrubs whose buds are elevated above the ground line to a height not exceeding about 25 cm., NANOPHANEROPHYTES = shrubs 25 to 200 cm. tall.

[9] The areal limits of Raunkiaer's (1934) leaf size classes are: LEPTOPHYLLS 25 mm.² or less, NANOPHYLLS 24-255 mm.² MICROPHYLLS 225-2,025 mm.², MESOPHYLLS 2,025-18,225 mm.²

outside source for its fruitless existence in the community. *Lomatium macrocarpum* belongs in the same category, except that it is a perennial, and the individuals may persist without reproducing for many years, unless competition is reduced by injury to the surrounding plants. All such plants are designated here as Class 1.

Class 2, which would be composed of species able to germinate, grow, and reproduce only vegetatively, is not represented in this association.

Class 3 is represented by Lithophragma and others which set very few seed. Their vigor in this association is not as great as it is elsewhere, and in the case of the therophytes in this group, the population density is maintained at least in part by means of seed produced outside of the climax association.

In Class 4 are the most successful species—those which generally set an abundance of seed each year.

BIOTIC CLIMAXES

Very few stands representative of the virgin Agropyronetum remain. The soils and rainfall in this zone are admirably suited for wheat production if the fields are left fallow in alternate years, so that most of the land has been brought under cultivation. The relatively small amount of grazing is restricted chiefly to the scablands which extend eastward well into this zone. A study of the effects of heavy spring-autumn sheep grazing upon the composition of the Agropyronetum of the scablands has been previously published (Daubenmire, 1940). Briefly, the changes brought about by overgrazing result in an elimination of Agropyron followed by an expansion of the annual flora to cover the ground. Sheep graze Poa very lightly in this region, and it remains to dominate the biotic climax.

On range lands which are grazed exclusively by cattle, such as the scarp just north of Lewiston, Idaho, it appears that a biotic climax dominated by *Bromus tectorum* and *Erodium cicutarium* is attained, although fire may be equally as important as grazing in maintaining this association.

OTHER PLANT ASSOCIATIONS WITHIN THE ZONE

FESTUCA ASSOCIATION

On the most protected slopes of the narrow ravines in the loessal areas, *Festuca idahoensis* dominates over all other species including Agropyron, which in this situation remains in the bunchgrass form. A few mesophytic forbs appear in this community and render it more distinctive: *Dodecatheon cusickii* Greene, and conspicuous amounts of Phlox and Brodiaea, both of which are present in small amounts in the climatic climax. *Poa ampla* Merr. is also conspicuous on these sites.

DISTICHLIS ASSOCIATION

By far the most abundant halophyte in the Agropyron-Poa zone is *Distichlis stricta,* although small amounts of Sarcobatus and Grayia occur locally. Not only does this grass predominate in shallow basins, but its presence at the foot of some slopes indicates otherwise unsuspected areas where saline seepage waters come near the surface. Occasionally Distichlis is associated with Elymus as an understory on flat slightly saline, valley bottoms.

ELYMUS ASSOCIATION

Valleys in the strictly loessal portion of the Agropyron-Poa zone are characteristically wide, shallow, and very flat. The original cover of these poorly drained silty soils was dominated by the giant bunchgrass *Elymus condensatus* (Fig. 10). This association attains its best development in the Agropyron-Poa zone, although it is found in all three zones. In the Agropyron-Poa zone it was probably second only to the Agropyronetum in area covered.

FIG. 10. *Elymus condensatus* growing in a flat valley bottom in the Agropyron-Poa zone between Washtucna and Kahlotus, Washington. Soil moisture studies were made here.

The ecology of Elymus is rather puzzling, for although it is primarily characteristic of poorly drained valley bottoms, it often colonizes railroad embankments which are well drained and seem to offer conditions for growth which are very different from those of the silty bottomlands.

ARTEMISIA-AGROPYRON ASSOCIATION

The Artemisietum extends far into the Agropyron-Poa zone along sandy valley bottoms, or on basalt outcroppings (Fig. 11). Both types of sites

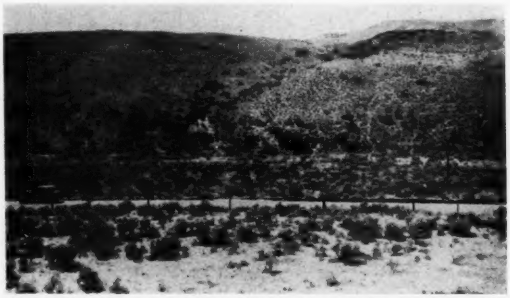

FIG. 11. *Artemisia tridentata* as an edaphic climax in a small valley north of Kahlotus, Washington. This shrub occupies the sandy alluvium of the valley bottom as well as the basalt outcrops along the sides of the valley. Here, in the Agropyron-Poa zone, Artemisia shows no tendency to invade the better upland soils even after all the Agropyron has been eliminated by overgrazing.

originated through glacio-fluvial action, so that this eastward extension of the Artemisietum is in the nature of edaphic climaxes which are practically confined to scablands.

The distributional pattern of the Artemisietum within the Agropyron-Poa zone is very irregular. Some valleys contain the association while others, appearing to offer identical ecological conditions, are completely devoid of the shrub.

CHRYSOTHAMNUS ASSOCIATION

Those areas of alluvial sands where the colloidal materials seem to be present in extremely small amounts support a permanent cover of the rabbit-brush community previously described (Figs. 8 and 12). Excessive drainage and deep soil seem to be key habitat factors for this association. A few Chrysothamnus plants occur in the Festuca-Agropyron zone, and there they are usually to be found in road cuts, which in the absence of sand deposits are about the only excessively drained sites in that zone.

FIG. 12. The Chrysothamnus stand east of Hooper, Washington where soil moisture studies were made. Due to overgrazing the few palatable herbs formerly in the association have been eliminated.

There seem to be no successional relationships between the three associations which have been described above as characteristic of valley bottoms in the Agropyron zone. Their distributions seem to be rigidly dictated by soil characteristics, especially water-retaining properties.

Preliminary measurements of readily available soil moisture in the summer of 1937 indicated considerable differences in this habitat factor among the more important associations in the Agropyron-Poa zone. During the subsequent year these studies were followed up by a series of simultaneous determinations of growth water in four associations on each of the dates indicated in Table 5.

The available soil moisture in the Agropyronetum was quite high in early April. By May 1 there had been a considerable reduction in the available moisture throughout the profile, but only in the upper 2 decimeters had the soil dried out. Three weeks later the zone of desiccated soil had extended down to a depth of about 4.5 decimeters. At this time the shallow-rooted annuals were mostly dormant and Agropyron was about to flower. On July 9 the water content had dropped slightly below the wilting coefficent throughout most of the upper meter of the profile, and the Agropyron spikelets had been matured and dropped. The fact that the leaves of this grass were still green and apparently functional indicated that the roots still had access to water, possibly below the meter level.

TABLE 5. Percent of available soil moisture in 4 plant associations in eastern Franklin County and adjacent Whitman County, Washington. Each figure was obtained by subtracting the wilting coefficient, as calculated from the hygroscopic coefficient (W. C. = H. C./0.68), from the actual moisture content of the soil.

Association and Status	Dm. Horizon	Apr. 8	May 1	May 22	July 9	Sep. 18	Total Range in Wilt. Coeffs.
	1	3.9	0.0	1.5	0.0	0.0	7.3–13.9
	2	7.4	0.7	0.0	1.8	0.0	7.7– 9.5
	3	5.9	2.3	0.0	0.0	0.0	8.1– 9.3
Agropyronetum	4	6.5	3.3	0.0	0.0	0.0	8.0– 9.1
(Climatic	5	7.0	3.8	....	0.3	0.0	7.0– 9.0
Climax)	6	6.4	4.1	2.3	0.7	0.0	6.6– 9.5
	7	7.4	4.3	....	0.0	0.0	7.2– 8.1
	8	6.4	4.9	3.3	0.0	0.0	7.4– 8.4
	9	....	5.1	....	0.0	0.0	7.2– 7.6
	10	6.3	6.0	....	0.0	0.0	7.7– 8.3
	1	12.0	0.0	0.4	0.0	0.0	4.6– 6.0
	2	5.9	6.4	0.0	0.0	0.0	4.0– 9.9
	3	6.9	4.5	2.7	1.3	0.0	4.4– 6.5
Artemisia	4	5.4	4.8	1.4	0.2	0.0	4.4– 6.4
Association	5	9.0	4.0	....	0.0	0.0	4.1– 7.6
(Edaphic	6	15.8	6.4	0.5	0.0	0.0	4.8–11.0
Climax)	7	7.9	6.7	....	0.0	0.0	4.8– 6.1
	8	7.4	6.8	1.3	0.0	0.0	4.5– 6.5
	9	5.6	8.0	....	0.0	0.0	4.6– 6.1
	10	5.6	....	....	0.0	0.0	5.4– 6.3
	1	19.1	0.0	2.9	0.0	0.0	4.9– 9.2
	2	18.0	2.5	1.3	1.3	0.0	4.9– 7.5
	3	17.1	4.2	4.6	0.0	0.0	4.1– 7.2
Chrysothamnus	4	18.4	5.2	7.1	0.4	0.0	3.5– 7.0
Association	5	18.7	5.9	....	0.5	0.0	3.0– 6.9
(Edaphic	6	20.8	6.9	10.0	0.4	0.0	2.6– 6.7
Climax)	7	20.8	7.0	....	0.0	0.0	2.3– 6.2
	8	22.4	6.8	11.0	0.1	0.0	2.4– 6.1
	9	22.7	....	....	0.6	0.2	2.4– 3.6
	10	20.8	8.0	....	2.6	0.0	3.8– 6.4
	1	....	....	3.4	0.0	0.0	17.6–19.8
	2	....	....	5.6	0.0	0.0	17.4–19.5
	3	....	....	4.5	0.0	0.0	11.7–12.7
Elymus	4	....	....	3.6	0.0	0.0	8.4–12.6
Association	5	....	....	....	0.0	0.0	11.0–11.3
(Edaphic	6	....	....	4.5	1.0	0.0	9.6–11.1
Climax)	7	....	....	....	0.8	0.8	8.2– 8.7
	8	....	....	12.0	0.8	0.6	6.0– 7.9
	9	....	....	....	1.2	0.4	7.1– 7.9
	10	....	....	....	0.0	0.9	7.0– 8.0

Throughout the summer and until sometime after September 18 the soil moisture content in this association dropped still further below the wilting coefficient and all plants in the Agropyronetum remained dormant. Since the weather during 1938 was not particularly abnormal, these data indicate that in general the upper meter of soil at this station is lacking in growth water for about 5 months beginning in late June.

The amount and seasonal distribution of available soil moisture in the Artemisietum are very similar

to conditions in the Agropyronetum, in so far as the upper meter of soil is concerned. The only important difference in the soils of these two communities in the Agropyron-Poa zone is the great difference in wilting coefficients. There is also a strong likelihood that in this valley there is subsoil moisture which is available to plants as deep rooted as Artemisia.

Data obtained in the Chrysothamnus association (Fig. 12) show great fluctuations in the moisture content of the soil as a result of local showers. During the season of 1938 the soil in this particular stand did not desiccate as rapidly as in the sagebrush stand under observation, but on the whole there is insufficient difference between these soils with regard to texture and water content to indicate the nature of the fundamental difference which evidently exists. The general preference of Chrysothamnus for sand and of Artemisia for a more fertile sandy loam suggests that fertility or perhaps soil temperature may be the critical environmental differences.

Soil conditions in the Elymus association are very different from those in the other three associations. The soil is fine textured, and horizons deeper than about 5 decimeters proved to contain growth water throughout the summer. The particular Elymus stand studied (Fig. 10) is located in the same valley as the Artemisia stand, a few kilometers to the west. The two studies in this valley suggest that gravitational water flows down the valley below the surface throughout the summer, and that local areas of fine-textured soil keep the water drawn up or dammed up near the surface. A high water table and poorly aerated soil generally favor Elymus rather than Artemisia, the latter of which is restricted to those parts of the valley where deep deposits of sand, or crevices in the basalt, allow the water to sink far below the surface and at the same time are sufficiently aerated that its roots can penetrate deeply enough to maintain contact with this moisture.

STREAMSIDE THICKETS

Salix, Cornus, Betula, Ribes and other ligneous genera contribute species to the tangled thickets which border the few permanent streams in the Agropyron-Poa zone.

THE FESTUCA-AGROPYRON ZONE

THE FESTUCETUM

When viewed from a distance, the Festucetum lacks the distinctive bunchy appearance of the Agropyronetum and appears as a rather uniform sward (Fig. 13), but close inspection of a stand reveals a dense profusion of showy-flowered forbs (Fig. 14) which renders this community far more varied than the other. At those times of the year when Balsamorhiza or Helianthella are in full flower, the blaze of yellow color makes the fence-corner relics of this association quite conspicuous, and indeed proved very useful in locating areas for study.

For the most part the lack of a bunchy aspect to the plant cover is due to the occupation of the spaces between the grasses by large forbs. Furthermore, in this association, *Agropyron spicatum* practically abandons the bunch habit and produces a distinct rhizome about 1 millimeter in diameter which gives rise to erect shoots at intervals of about 2 to 3 centimeters. Accompanying this change in morphology is a reduction in the number of inflorescences produced by each plant.[10] Both of these characteristics of Agropyron tend to promote uniformity in the physiognomy of the plant cover.

Of all three climatic climax associations in southeastern Washington, this has the least variation in structure throughout its extent, even though it occurs in two distinct regions which are separated by communities of the Agropyron-Poa zone (Fig. 1).

FIG. 13. One of the virgin areas of Festucetum which has been used for frequency, constancy, and other sociologic studies. Located at the east edge of Pullman, Washington. Photograph taken in May with camera pointed ESE. Note the barchane-like shape of this loessal hill and the rolling nature of the topography. On the north-facing slope is a deciduous thicket dominated by Rosa, Symphoricarpos, Prunus, and *Crataegus douglasii*. A similar thicket has sprung up along the fence which follows the profile of the hill.

FIG. 14. Detail of the Festucetum at the same station as Fig. 13. The large grayish leaves are Balsamorhiza. The composite in flower is Helianthella. The elongate congested inflorescences to the right of the stake are Castilleja. In the middle foreground are the palmate leaves of Potentilla. On this date, June 1, Agropyron inflorescences were well developed.

[10] In mid-June sample plots measuring 1 x 10 meters were measured off in a stand of Festucetum and a stand of Agropyronetum (on thin soil), both of which are located in Whitman County, Washington. The Agropyron in these two plots was then clipped to the ground line, flowering and vegetative shoots separated, and all material oven-dried and weighed. The flowering shoots, expressed as a percentage of total shoots, constituted 40.5 percent and 3.6 percent, respectively, of material in the Agropyron-Poa and the Festuca-Agropyron association.

In the Blue Mountain sector, the writer has seen no Iris in the uplands, although this plant is characteristic of the Bitterroot region. Also it was observed that locally the characteristic *Lupinus sericeus* may be lacking in the community, but its place seems always taken by another species in the same genus, such as *L. laxiflorus* or *L. sulphureus* Dougl.

In the ecotone between the Agropyronetum and the Festucetum, these two associations alternate with each other on slopes having different exposures. As criteria for the absolute distinction of these two associations the following were used: (1) the absence of *Poa secunda* and *Plantago purshii,* and (2) the presence of certain species which were found to have high constancy in the Festucetum (*Calochortus elegans, Clematis hirsutissima, Erythronium grandiflorum, Frasera albicaulis, Haplopappus liatriformis, Orthocarpus tenuifolius, Senecio columbianus, Solidago missouriensis, Viola adunca,* and *Zygadenus gramineus*). Either phenomenon is believed to be a good indicator of the former existence of Festucetum in stands located near the ecotone where the vegetation has been considerably disturbed.

CONSTANCY

Five of the 14 stands used for constancy studies are on fairly level portions of the topography, and the others are on slopes facing N, NNW, WNW, W, S, SE, or E. The elevation of the lowest stand is 762 meters and the highest 841 meters above sea level. They are divided among Whitman County, Washington, and Latah and Nez Perce Counties, Idaho.

In Table 6 all the vascular plants encountered are listed according to the synusiae to which they belong. The only species attaining a constancy of 14/14 in both the Agropyronetum and the Festucetum is *Agropyron spicatum.* Although more than twice as many species were encountered in the Festucetum series, the number of species with 14/14 constancy is approximately the same as in the Agropyronetum. The greater richness in species of the Festucetum is reflected by the following points of comparison:

Comparisons	*Agropyronetum*	*Festucetum*
Minimum number of species per plot	13	26
Maximum number of species per plot	21	42
Average number of species per plot	17.4	32.4
Total number of species encountered	35	77

A study of the field data with respect to the incidence of species with reference to slope exposure brought out two facts of interest. A group of perennial forbs is rare or lacking on south-facing slopes: *Clematis hirsutissima, Erythronium grandiflorum, Sieversia ciliata, Viola adunca,* and *Zygadenus gramineus.* Secondly, a group of annuals seldom were encountered on north-facing slopes: *Bromus mollis, B. tectorum, Draba verna,* and *Veronica arvensis.* Other effects of slope exposure could undoubtedly be demonstrated by studies of the density rather than the incidence of species at the various stations.

TABLE 6. Constancy of vascular plants in 14 stands of the Festucetum. Species with the same constancy and in the same synusia are listed alphabetically.

TALL HERB SYNUSIA	
Agropyron spicatum (Pursh) Scribn. & Smith	14
Festuca idahoensis Elmer	14
Balsamorhiza sagittata (Pursh) Nut.	11
Sidalcea oregana (Nutt.) Gray	3
Sphenopholis obtusata (Michx.) Scribn.	1
INTERMEDIATE HERB-SHRUB SYNUSIA	
Achillea lanulosa Nutt.	14
Hieracium albertinum Farr.	14
Potentilla blaschkeana Turcz.	14
Lupinus sericeus Pursh	13
Symphoricarpos albus (L.) Blake	13
Epilobium paniculatum Nutt.	12
Haplopappus liatriformis (Greene) St. J.	12
Koeleria cristata (L.) Pers.	12
Lomatium triternatum (Pursh) C. & R.	12
Rosa spp.*	12
Besseya rubra (Dougl.) Rydb.	11
Helianthella douglasii T. & G.	11
Lithospermum ruderale Dougl.	11
Poa pratensis L.	11
Senecio columbianus Greene	10
Bromus mollis L.	10
Brodiaea douglasii Wats.	9
Calochortus elegans Pursh	9
Carex geyeri Boott	9
Castilleja lutea Heller	9
Geranium viscosissimum Fisch. & Mey.	9
Sieversia ciliata (Pursh) G. Don	9
Iris missouriensis Nutt.	8
Solidago missouriensis Nutt.	8
Galium boreale L.	7
Erigeron corymbosus (H. & A.) T. & G.	6
Lithophragma parviflora (Hook.) Nutt.	6
Astragalus arrectus Gray	5
Fritillaria pudica (Pursh) Spreng.	5
Gaillardia aristata Pursh	5
Zygadenus gramineus Rydb.	5
Clematis hirsutissima Pursh	4
Bromus tectorum L.	3
Erythronium grandiflorum Pursh	3
Leptotaenia multifida Nutt.	3
Prunus melanocarpa (Nels.) Rydb.	3
Ptilocalais nutans (Geyer) Greene	3
Allium geyeri Wats.	2
Apocynum pumilum (Gray) Greene	2
Astragalus spaldingii Gray	2
Berberis repens Lindl.	2
Bromus brizaeformis Fisch. & Mey.	2
Festuca pacifica Piper	2
Juncus balticus Willd.	2
Phleum pratense L.	2
Sisymbrium altissimum L.	2
Sisyrinchium inflatum (Suksd.) St. J.	2
Antennaria luzuloides T. & G.	1
Calochortus sp.**	1
Frasera albicaulis Dougl.	1
Fragaria sp.**	1
Galium (triflorum?)**	1
Heuchera glabella T. & G.	1
Lupinus laxiflorus Dougl.	1
Orthocarpus tenuifolius (Pursh) Benth.	1
Potentilla glandulosa Lindl.	1
Sanguisorba occidentalis Nutt.	1
Silene douglasii Hook.	1
Spiraea lucida Dougl.	1
LOW HERB SYNUSIA	
Collinsia parviflora Lindl.	13
Draba verna L.	10
Gilia gracilis Hook.	9
Claytonia linearis Dougl.	7
Stellaria nitens Nutt.	4
Veronica arvensis L.	4
Viola adunca Sm.	4
Cirsium sp.**	3
Lithophragma bulbifera Rydb.	3
Claytonia parviflora Dougl.	2
Alyssum alyssoides L.	1
Lactuca sp.**	1
Lomatium macrocarpum (H. & A.) C. & R.	1
Ranunculus glaberrimus Hook.	1
Total species:	78

*Includes several species which seem to be identical ecologically, and are difficult to separate taxonomically.
**The identity of certain species which were never found flowering in the virgin prairie is questionable.

Ninety-five species were encountered in the constancy studies of both the Agropyronetum and the Festucetum. Of these, 17 species are common to both associations. The Agropyronetum is composed of the most xerophytic species of the Festucetum to which a few exclusives (especially *Agoseris glauca, Plantago purshii,* and *Poa secunda*) are added. The Festucetum contains nearly all of the larger species

of the Agropyronetum, and in addition has a great number (60) of near-exclusive species, most of which are large mesophytic perennials.

MINIMAL AREA

The species in this association are so evenly distributed that the minimal area for floristic studies is attained very quickly. To illustrate this point, two of the 1 x 10 meter constancy strips in each of two widely separated stands were subdivided into meter-square units. For each strip, a complete list was first made of the flora of one of the end subdivisions. Then in the adjacent subdivision a list was made of those species not encountered in the first, and the same procedure was followed with successive subdivisions in turn. It is evident from Table 7 that

Table 7. The minimal area data for two stands of Festucetum, based on floristics.

Strip	Subdivisions										Total
	1	2	3	4	5	6	7	8	9	10	Species
A	22[1]	2[2]	0	0	0	1	1	0	1	2	29
B	24	2	3	0	0	1	0	1	0	0	31

[1] Twenty-two species occurred in the first square meter of Strip A.
[2] Two additional species were encountered in the second square meter, and so on.

the great bulk of the species in the stand is encountered in a single, random, meter-square plot, and that by increasing this initial area as much as 1,000 percent the floristic list is increased but little.

Homologous studies were not made in the Agropyronetum, but due to the lesser floristic complexity of that association, a 1 x 10 meter plot probably exceeds the minimal area there more than it does in the Festucetum.

SYNUSIAE

There may be recognized the following synusiae:

1. moss-lichen synusia
2. low herb synusia (mostly under 10 cm. in height)
3. intermediate herb-shrub synusia (10-60 cm. tall)
4. tall herb synusia (60-80 cm. in height)
5. endophyllous fungal synusia.

During the rainy winter season when most of the vascular plants possess but immature shoots, patches of bright green mosses are evident beneath the herbs. The mosses have considerably higher coverage than their lichen associates, but both types of plants cover less than half of the interstitial space between the larger plants. During the dry summer these cryptogams are entirely dormant and quite inconspicuous.

Just as in the Agropyronetum, the great majority of species in the low herb synusia are annuals, whereas the taller phanerogamous synusiae are composed chiefly of perennials. However, similarity does not extend beyond this point, for the low herb is the least complex of the Festucetum synusiae (Table 6), whereas it is the most complex layer in the Agropyronetum. The paucity of small annuals in the Festucetum is probably due to their relatively high light requirements not being met beneath the fairly dense and nearly continuous canopy formed by the large perennial herbs.

By far the majority of species belong in the intermediate herb-shrub synusia. Most of these plants are perennial herbs, although a few are annuals and a few are shrubs. Rosa and Symphoricarpos are represented by dwarfed, inconspicuous individuals well scattered through the prairie. In this association these shrubs flower and fruit very sparingly, whereas in adjacent shrub thickets where they are the dominants, they attain much greater size and reproductive vigor.

In virgin prairie the leaves of a great many species are parasitized by fungi during the summer. This phenomenon is more pronounced in the Festucetum than in any other North American prairie region which the writer has seen.

FREQUENCY

Two fairly large virgin stands of the Festucetum were discovered in Whitman County, Washington, at a distance of about 8 kilometers from each other. One hundred frequency plots were established in each stand and studied in a manner similar to that pursued in the Agropyronetum (Table 8).

In comparing the data for the two associations it is interesting to note that Agropyron has about the same frequency in both associations, but in the Festucetum its frequency is greatly exceeded by that of Festuca, which plays a very minor role in the more xeric zone.

DOMINANCE

Clippings for dominance statistics were made near Pullman, Washington, in a manner identical to that followed in the other prairie type. Dominance data for the Festucetum (Table 9) and the Agropyronetum (Table 4) are summarized and compared in Table 10.

The most striking contrasts between the two associations are: (1) the greater dry weight of shoots produced annually by the Festucetum, (2) the dominance of forbs over grasses in the Festucetum as contrasted with the reverse situation in the Agropyronetum, and (3) the presence of a dwarf shrub element in the Festucetum, whereas it is not represented in the Agropyronetum.

PERIODICITY

The period of vegetative aestivation is of shorter duration in the Festucetum than in the Agropyronetum, a fact which seems due to the more favorable water balance of the upper altitudinal zone. The higher rainfall and lower evaporation in the Festuca-Agropyron zone not only allows the supply of soil moisture to last farther into the summer, but permits the soil to become moistened sufficiently for the resumption of plant growth at an earlier date in the fall than is the case in the Agropyron-Poa zone. By about the middle of July only 19 percent of the Agropyronetum species listed in Table 4 still possess actively photosynthetic organs, whereas in the Festucetum the homologous figure is 60 percent. On the whole, the period of vegetational aestivation is about 1/3 to 1/2 as long in the Festucetum as in the

TABLE 8. Frequency of vascular plants in two virgin stands of the Festucetum. In each stand 100 plots, 2 x 5 decimeters each, were arranged in two parallel rows, with the rows and the plots in each row separated by one meter.

Species	A	B	Mean
Festuca idahoensis	98%	99%	98.5%
Agropyron spicatum	87	74	80.5
Helianthella douglasii	59	86	72.5
Collinsia parviflora	42	85	63.5
Brodiaea douglasii	64	50	57.0
Haplopappus liatriformis	68	43	55.5
Calochortus elegans	37	71	54.0
Poa pratensis	53	55	54.0
Lupinus sericeus	59	48	53.5
Bromus mollis	12	77	44.5
Draba verna	16	73	44.5
Potentilla blaschkeana	77	10	43.5
Astragalus arrectus	0	85	42.5
Achillea lanulosa	25	47	36.0
Stellaria nitens	3	65	34.0
Symphoricarpos albus	17	50	33.5
Balsamorhiza sagittata	30	30	30.0
Gilia gracilis	20	30	25.0
Besseya rubra	0	48	24.0
Claytonia parviflora	0	46	23.0
Senecio columbianus	24	20	22.0
Claytonia linearis	2	34	18.0
Epilobium paniculatum	22	6	14.0
Hieracium albertinum	9	14	11.5
Galium boreale	0	21	10.0
Sisyrinchium inflatum	0	20	10.0
Rosa spp.	0	19	9.5
Erigeron corymbosus	19	0	9.5
Carex geyeri	18	0	9.0
Castilleja lutea	8	8	8.0
Lactuca sp.	2	13	7.5
Iris missouriensis	0	14	7.0
Lithophragma bulbifera	9	2	5.5
Lomatium triternatum	5	4	4.5
Zygadenus gramineus	2	7	4.5
Sieversia ciliata	5	1	3.0
Koeleria cristata	1	5	3.0
Geranium viscosissimum	6	0	3.0
Bromus brizaeformis	4	1	2.5
Astragalus spaldingii	4	0	2.0
Calochortus sp.	0	4	2.0
Frasera albicaulis	0	3	1.5
Erythronium grandiflorum	0	3	1.5
Lithophragma parviflora	0	3	1.5
Solidago missouriensis	0	2	1.0
Lithospermum ruderale	1	1	1.0
Fritilaria pudica	2	0	1.0
*Bromus tectorum**	1	0	0.5
Ptilocalais nutans	1	0	0.5
Total species encountered	37	42	

*A solitary individual growing in the freshly disturbed soil at the entrance to a ground squirrel burrow.

Agropyronetum. The significance of the more favorable moisture balance in the Festuca-Agropyron zone is also reflected in current agricultural practice. Here, there is adequate moisture to produce wheat every year, although a rotation of peas and wheat is usually practiced.

In the Festucetum, flowering is initiated in the spring by Carex and Besseya which flower about the first week in April, but in the Agropyronetum the flowering of Draba, Lithophragma, and Ranunculus has begun about 3 weeks earlier. Likewise the general period of flowering endures farther into the summer in the Festucetum. Flowering in the Agropyronetum practically ceases after the first week in June, but in the Festucetum 10 of the 50 species listed in Table 9 are usually still in flower by the middle of July.

The fact that the period of flowering for the community as a whole is later in the Festucetum may be due to the coolness of the climate at the higher alti-

TABLE 9. Some sociological characteristics of those species of the Festucetum having a constancy in excess of 2/14 (see Table 6).

Species	Constancy	Life Form	Leaf Size	Vitality Class	Dominance*
Achillea lanulosa	14	hemicryptophyte	leptophyll	3	99
Agropyron spicatum	14	hemicryptophyte	nanophyll	3	566
Astragalus arrectus	5	hemicryptophyte	nanophyll	4	1,111
Balsamorhiza sagittata	11	geophyte	mesophyll	4	2,955
Besseya rubra	11	geophyte	microphyll	4	29
Brodiaea douglasii	9	geophyte	nanophyll	1	32
Bromus mollis	10	therophyte	nanophyll	4	1,245
B. tectorum	3	therophyte	nanophyll	4	
Calochortus elegans	9	geophyte	microphyll	4	8
Carex geyeri	9	geophyte	nanophyll	4	
Castilleja lutea	9	hemicryptophyte	microphyll	4	186
Cirsium sp.	3	hemicryptophyte	microphyll	1	
Claytonia linearis	7	therophyte	leptophyll	4	
Clematis hirsutissima	4	geophyte	nanophyll	4	
Collinsia parviflora	13	therophyte	nanophyll	4	42
Draba verna	10	therophyte	leptophyll	4	
Epilobium paniculatum	12	therophyte	nanophyll	1	
Erigeron corymbosus	6	hemicryptophyte	microphyll	3	
Erythronium grandiflorum	3	geophyte	mesophyll	4	
Festuca idahoensis	14	hemicryptophyte	nanophyll	4	4,747
Fritillaria pudica	5	geophyte	microphyll	4	
Gaillardia aristata	5	geophyte	microphyll	4	
Galium boreale	7	hemicryptophyte	nanophyll	4	32
Geranium viscosissimum	9	hemicryptophyte	mesophyll	4	
Gilia gracilis	9	therophyte	leptophyll	4	3
Haplopappus liatriformis	12	hemicryptophyte	microphyll	4	684
Helianthella douglasii	11	hemicryptophyte	microphyll	4	9,158
Hieracium albertinum	14	geophyte	microphyll	4	560
Iris missouriensis	8	geophyte	microphyll	3	
Koeleria cristata	12	geophyte	nanophyll	4	40
Leptotaenia multifida	3	geophyte	leptophyll	4	29
Lithophragma bulbifera	3	geophyte	leptophyll	2	1
L. parviflora	6	geophyte	nanophyll	3	
Lithospermum ruderale	11	geophyte	microphyll	4	85
Lomatium triternatum	12	geophyte	nanophyll	4	3
Lupinus sericeus	13	geophyte	microphyll	4	1,042
Poa pratensis	11	hemicryptophyte	nanophyll	4	10
Potentilla blaschkeana	14	hemicryptophyte	microphyll	4	89
Prunus melanocarpa	3	nanophanerophyte	microphyll	1	
Ptilocalais nutans	3	geophyte	nanophyll	4	
Rosa, spp.	12	chamaephyte	nanophyll	3	717
Senecio columbianus	10	geophyte	mesophyll	3	
Sidalcea oregana	3	hemicryptophyte	mesophyll	4	
Sieversia ciliata	9	hemicryptophyte	nanophyll	4	
Solidago missouriensis	8	hemicryptophyte	microphyll	4	
Stellaria nitens	4	therophyte	leptophyll	4	6
Symphoricarpos albus	13	chamaephyte	microphyll	3	614
Veronica arvensis	4	therophyte	leptophyll	4	
Viola adunca	4	hemicryptophyte	nanophyll	4	
Zygadenus gramineus	5	geophyte	nanophyll	4	

*Figures refer to oven-dry weight of shoots in grams per 1,000 square meters.

TABLE 10. Comparisons of the relative dominance of different life forms in two prairie types.

Groupings	Oven-dry weight of shoots per 1,000 sq. m.	
	Festucetum	*Agropyronetum*
Annual Herbs	1,254 g.	461 g.
Perennial Herbs	21,508	9,437
Shrubs	1,331	0
Grasses	6,608	9,646
Forbs	16,154	252
Shrubs	1,331	0
Totals	24,093	9,898

tude, or it may be that the species which compose this association are by nature late-flowering and possibly for this reason are kept out of the Agropyronetum. That the former hypothesis is true for at least some of the species is indicated by the fact that in those species common to both associations, flowering is generally 1 to 3 weeks later in the Festucetum.

LIFE FORM CLASSES

The life form data for both prairie associations may be summarized and compared as follows:

	Agropyronetum percent	*Festucetum* percent
therophytes	52	18
geophytes	30	42
hemicryptophytes	15	34
chamaephytes	4	4
nanophanerophytes	0	2

The percentage of therophytes is very much lower in the more mesophytic association, and this is compensated by an increase in geophytes and chamaephytes, both of which are less efficient in evading the rigors of a long dry season than are therophytes.

LEAF SIZE CLASSES

A comparison of the two climax prairie types from the standpoint of leaf size classes is as follows:

	Agropyronetum percent	*Festucetum* percent
leptophylls	48	16
nanophylls	41	40
microphylls	11	34
mesophylls	0	10

The tendency for the leaves (or leaflets) to have larger individual areas in the more mesophytic association is very pronounced.

VITALITY

Four members of the Festucetum, Brodiaea, Cirsium, Epilobium, and Prunus, seem unable to reproduce sexually or asexually in this association in average years. The percentage of species in the various vitality classes (Table 9) is very similar in both the Agropyronetum and the Festucetum.

EFFECT OF FIRE ON THE FESTUCETUM

Although prairie fires are rare in the Palouse, several opportunities were presented to observe the effects of intentional burning of virgin prairie. Fire eliminates the moss-lichen synusia, and its redevelopment requires at least several years. Perennial grasses and forbs and the shrubs are killed to the ground but in practically all cases they sprout up vigorously the following spring. In fact, this new growth on burned areas makes its appearance about 2 weeks earlier than on unburned areas, presumably the result of greater absorption of solar radiation by the blackened, unshaded soil surface.

OTHER PLANT ASSOCIATIONS WITHIN THE ZONE

STREAMSIDE THICKETS

Stream courses in all but the smallest valleys in the Festuca-Agropyron zone formerly supported a fringe of low trees (Fig. 15), principally *Crataegus*

FIG. 15. Streamside thicket of *Crataegus douglasii*, and lowland meadow, in the Festuca-Agropyron zone a few kilometers south of Moscow, Idaho. The flat-topped inflorescences belong to *Achillea lanulosa*, the racemose inflorescences to *Lupinus leucophyllus*, and the composite in the lower right corner is *Gaillardia aristata*.

douglasii Lindl., *Salix* spp., *Betula microphylla* Bunge., *Alnus tenuifolia* Nutt., and *Amelanchier florida* Lindl. Locally *Populus tremuloides* Michx. or *Pinus ponderosa* Dougl. formed stands on floodplains or on the north-facing slopes of these valleys. Stands of Populus and Pinus at present extend well out into all three zones in the northern part of southeastern Washington.

LOWLAND MEADOWS

Floodplains of the wider valleys appear to have been too moist for the climatic climax, yet insufficiently sheltered by the remoteness of the bluffs to allow the streamside forest to spread far from the water course. Such open lowlands supported a rank growth of grasses and forbs which comprised a floristically complex community (Fig. 15). Some characteristic species are: *Camassia quamash* (Pursh) Greene, *Brodiaea douglasii*, *Wyethia amplexicaulis* Nutt., *Iris missouriensis* in dense pure populations, *Calochortus pavonaceus* Fern., *Juncus balticus* Willd., *Heracleum lanatum* Michx., *Castilleja miniata* Dougl., *Lupinus leucophyllus* Dougl., *Delphinium strictum* A.

Nels., *Polygonum bistortoides* Pursh and *Poa ampla* Merr. The farinaceous bulbs of Camassia were a staple food of the Amerinds who annually dug them in great numbers as the plants withered in June or July.

There appear to have been relatively small amounts of *Elymus condensatus* in this zone. The remaining relics indicate that originally the species was represented locally in the ecotone between the meadow and the climatic climax prairie of the uplands.

With practically all of the upland in the Festuca-Agropyron zone devoted to agriculture, the chief pasture areas consist of the lowland meadows. These escaped cultivation chiefly because of their meandering stream courses and their wetness in spring. Under heavy grazing the original meadow association is replaced by a nearly pure stand of *Poa pratensis,* which by overgrazing is in turn replaced by communities of tall unpalatable forbs: *Artemisia absinthium* L., *Dipsacus sylvestris* Huds., *Cirsium* spp., *Tanacetum vulgare* L., *Arctium minus* (Hill) Bernh., etc.

ROSA-SYMPHORICARPOS ASSOCIATION

Deciduous thickets dominated by these two genera become very abundant on protected upland slopes (Fig. 13), especially near the edge of the timbered foothills. Here a high percentage of the non-forested area is covered by scrub rather than by the Festucetum. The thickets are dense, and vary from a half to one and one-half meters in height. On the most mesic sites these shrubs are accompanied by taller shrubs such as *Prunus melanocarpa, Crataegus douglasii,* and *Amelanchier florida.* Characteristic forbs of the association are: *Agastache urticifolia* (Benth.) Kuntze, *Veratrum speciosum* Rydb., and *Chamaenerion angustifolium* (L.) Scop.

Apparently there is a very narrow margin of difference between those habitats which foster the development of the Rosa-Symphoricarpos and Festuca-Agropyron associations. Wherever a three-strand barbed wire fence is stretched across a stand of Festucetum, a narrow strip of thicket replaces the prairie along the fence (Fig. 13). The species of shrubs are the same as those which are abundantly represented throughout the prairie as dwarfed individuals. It appears that the action of the wire in slowing down the velocity of the wind which results in a deposition of snow in winter and dust in summer, is sufficient to throw the moisture balance in favor of the shrubby members of the prairie community. Symphoricarpos is greatly favored by a slight covering of the original soil surface by rodent excavations, and it may be that dust deposition alone is sufficient to throw the balance in favor of the scrub community. Once the fencerow thicket develops, the interception of dust is more complete so that the soil level on the windward side of the fence may be built up half a meter higher than on the leeward side.

AGROPYRON-POA ASSOCIATION

The transfer of dust from windward to leeward slopes of hills often prevents the accumulation of a deep soil over the basalt along the upper extremities of windward slopes and bluffs. These areas where the loessal mantle is but a few decimeters in depth support a community closely similar to the typical Agropyronetum previously described. The chief characteristics which distinguish this edaphic climax (or perhaps stage in a xerosere) from the climatic climax to the west are (1) the practically complete absence under undisturbed conditions of many annuals found in the Agropyronetum: Plantago, *Festuca pacifica,* Erodium, Plagiobothrys, Madia, Sisymbrium, and (2) the presence of a scattering of forbs or shrubs drawn from the Festucetum.

BEHAVIOR OF EXOTIC SPECIES IN CLIMAX COMMUNITIES

Climax communities are the final products of environmental complexes, the component forces of which have long been at work sorting out and eliminating certain species but preserving others which are successful in each particular habitat. Competition increases to a high level in such a community since only those plants have persisted which possess a great amount of endurance to crowding. Furthermore, every synusia has had a long period in which to become "saturated" with immigrants. By means of peculiarities of life form and periodicity, late arrivals in a habitat are sometimes able to evade much of the force of competition from plants previously established by playing roles complementary to the latter. From the standpoint of plant sociology, the role of exotic species which immigrate into a climax community is consequently of considerable interest.

In the analyses of virgin and near-virgin climax prairies of the Palouse region, a grand total of 93 species was encountered in the constancy plots. Of these, nine (10 percent) are exotics derived indirectly from Eurasia in the last few decades: *Alyssum alyssoides, Bromus brizaeformis, B. mollis, B. tectorum, Erodium cicutarium, Phleum pratense, Poa pratensis, Sisymbrium altissimum,* and *Veronica arvensis.*

Instances where introduced species insert themselves successfully into a climax are not abundant. In the Agropyronetum, *Bromus tectorum,* with a constancy of 14/14 is an outstanding example of such a case.

A statement to the effect that Bromus is to be considered a true member of the climax Agropyronetum would seem jeopardized at the outset by the fact that all of the stands studied have been subjected to at least a small amount of grazing at some time in the past. However, the evidence which leads the writer to believe in its climax status is as follows.

In 1911 a railroad was built parallel to the Palouse River canyon (Fig. 4) in Franklin County, Washington. To maintain a fairly level track it was necessary in places to excavate a trench 5 meters or more in depth. These deep cuts completely isolated from

the remainder of the prairie several spurs of the upland which extend toward the river at right angles to the railroad. Prior to the construction of this road, the region was too sparsely settled for the grass to have suffered much from cattle grazing. Today several of these isolated buttes are covered with beautiful stands of Agropyronetum which have been absolutely protected from grazing for a continuous period of 30 years. These stands all have a small, evenly distributed population of *Bromus tectorum,* whose life form and periodicity is significantly identical to that of the indigenous annuals of the same synusia. It seems safe to assume that under 30 years of complete protection Bromus should have been completely eliminated, at least in the heaviest stands of the Agropyronetum, if such had been possible. Since it has held its ground, and is thriving as well as (or better than some of) the indigenous species of similar life form, the writer considers it a thoroughly naturalized alien here. It will be recalled that this grass is also represented in the Lamont cemetery which has been under protection for at least 50 years.

Many near-virgin stands of Agropyronetum located in other regions were examined. Although these had suffered varying degrees of grazing in recent years, the amount of *Bromus tectorum* is approximately equal in these lightly grazed stands to the amount on the long-isolated buttes. From the close similarity between these widely scattered, lightly grazed stands and areas of long protection, it may be concluded that the persistence of this annual in the Agropyronetum does not depend upon continued grazing. In fact, detailed studies have shown that its abundance decreases rapidly under spring-autumn sheep grazing (Daubenmire, 1940).

The heaviest stands of Bromus in this region occur on disturbed soils such as abandoned fields, or on overgrazed areas where grazing pressure in the spring has been reduced. In such habitats it relinquishes its dominance very slowly, apparently due to an ability to compete successfully with seedlings of perennial grasses. Such agressiveness on the part of a small annual suggests that the climate of the Pacific Northwest is ideally matched with the requirements of the plant. Hitchcock (1935) states that although this species has been introduced into most of the United States, it is most abundant in Washington and Oregon.

Erodium has invaded the same climax prairie, but its sparsity, dwarf form, and quick response to release from competition show that it is not as much at home in the Agropyronetum as is Bromus.

In the Festucetum, *Phleum pratense, Bromus mollis, Poa pratensis,* and *Veronica arvensis* seem to have become a part of the climax community. There seems to be little question about the climax status of the last three of these plants, for many of the relics of the Festucetum which contain them are in perfect condition.

It will be noticed that only two exotic species have invaded the Agropyronetum while four occur in the Festucetum. Perhaps this may be accounted for by the more severe environment of the Agropyronetum which is so exacting in its demands upon the plants that fewer exotics qualify for a place in the community.

In an entirely different category are those plants which enter the climax prairie only where the soil has been locally disturbed, as around a rodent burrow. Apparently the killing out of a single large dominant reduces the competition sufficiently so that a few individuals of these exotic species can germinate and grow to maturity. If elsewhere in the community they are able to germinate, the seedlings perish before attaining recognizable size. *Alyssum alyssoides, Bromus tectorum, B. brizaeformis,* and *Sisymbrium altissimum* all play such a role in the Festucetum, and the last named occurs in disturbed Agropyroneta as well. The unidentified Cirsium (Festucetum) and Lactuca (Festucetum and Agropyronetum) listed in the constancy tables may belong to this category if the specimens represent exotic species, but they may just as well belong to indigenous species of similar ecological status. All of the four annuals mentioned above are characteristic of temporary communities of secondary seres where exotics are usually on more nearly equal terms with indigenous floras. They may be considered as good indicators of disturbance because of the readiness with which they enter even the smallest disturbed spots.

The tall forbs which dominate overgrazed lowland meadows in the Festuca-Agropyron zone are also Eurasian immigrants.

AFFINITIES OF THE VEGETATION

FLORISTIC AFFINITIES

The bulk of the modern flora of southeastern Washington appears to have immigrated into the area since the change in climate which was occasioned by the elevation of the Cascades. Prior to this event, arid climates and xerophytic vegetation had long existed in regions to the south and east, so that the population of arid Washington by immigration from the older xerophytic floras became possible wherever suitable migratory routes existed. The chief avenue for plant immigration was the gap in the encircling mountains which exists between the Blue and Cascade Mountains. For this reason the bulk of the xerophytic flora of southeastern Washington might be expected to have stemmed from the desert plateaus of the intermountain region[11] which are in direct contact with eastern Washington by way of this migratory route.

In an attempt to discover the various sources of the flora, and to evaluate the relative importance of these, studies of the distributions of 20 indigenous species were made. Five species were selected from each of the three major zones in southeastern Washington. These choices were intended to be species more or less restricted to one particular zone. An

[11] In this paper the term "intermountain region" is used to indicate the area between the Sierras and the Rockies, from northern Arizona to southern Idaho and eastern Oregon.

additional group of five species was chosen to include plants ranging widely through two or more of these zones. In all cases the selection of species for study was influenced by their relative importance in southeastern Washington, rather than a deliberate attempt to demonstrate any preconceived notions of floristic affinities.

The ranges of the five species selected as representative primarily of the Artemisia-Agropyron zone are very similar (Fig. 16). They suggest an important center of distribution in the Nevada region, and from this center desert species have migrated northward around the west end of the Blue Mountains into southeastern Washington. Based on a knowledge of

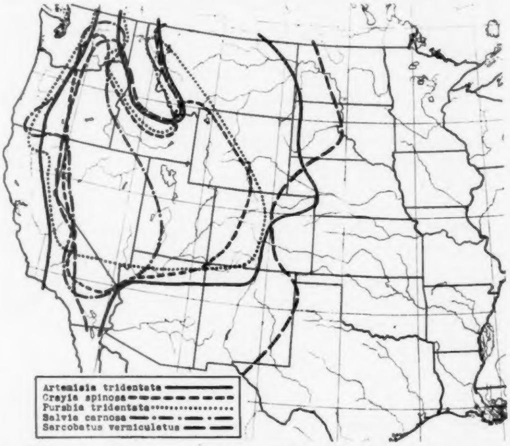

FIG. 16. Ranges of five species selected as the most important indigenous species which are characteristic primarily of the Artemisia-Agropyron zone in southeastern Washington.

plant ranges as understood prior to 1906, Piper (1906) listed 87 species of the Artemisia-Agropyron zone as having entered Washington from the intermountain region, and 16 which appear to have crossed the Sierras and Cascades from regions west of those mountains.

Greater diversity is displayed in the ranges of the five species representing the Agropyron-Poa zone (Fig. 17). *Festuca pacifica, Madia exigua,* and *Plagiobothrys tenellus,* all of which are subordinate therophytes in the Agropyronetum, seem to have a west-coast center of distribution. A strongly contrasted range is that of *Plantago purshii* which appears to have entered Washington from the east or southeast. The range of *Poa secunda* is rather intermediate in position, and its source is not clear from such data.

The five species selected as characteristic of the Festuca-Agropyron zone contrast strongly with all other groups considered in matters of extent and centers of distribution (Fig. 18). These ranges center about the eastern Palouse (Festuca-Agropyron zone), and the species show a higher degree of endemism than any of the other 15 species which are mapped.

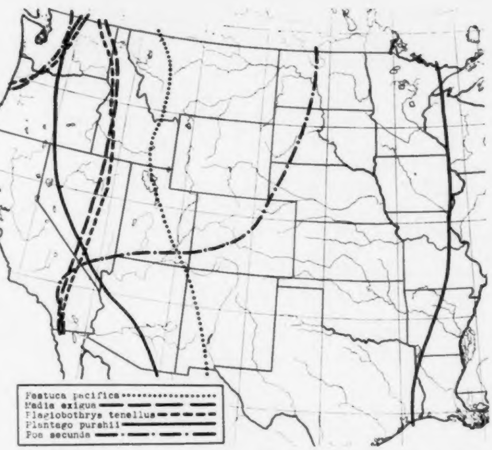

FIG. 17. Ranges of five species selected as the most important indigenous species which are characteristic primarily of the Agropyron-Poa zone in southeastern Washington.

Among those species which range entirely across the unforested plateau from the Bitterroots to the Cascades, centers of origin are least apparent. The ranges of *Festuca idahoensis* and *Agropyron spicatum* center about the Bitterroots, while the other three species have a wide range—from the west coast to the plains east of the Rockies.

The distributions of these 20 species selected as characteristic of the vegetation of southeastern Washington show that the flora is a polyphyletic mixture of species drawn from the intermountain region, from the plains east of the Rockies, and from the coastal region west of the Sierras, together with species more or less endemic to the Palouse region. Of all these sources, the intermountain region probably has supplied the most species.

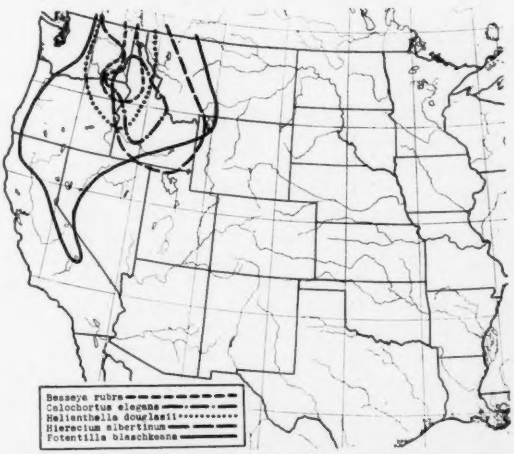

FIG. 18. Ranges of five species selected as the most important indigenous species which are characteristic primarily of the Festuca-Agropyron zone in southeastern Washington and adjacent Idaho.

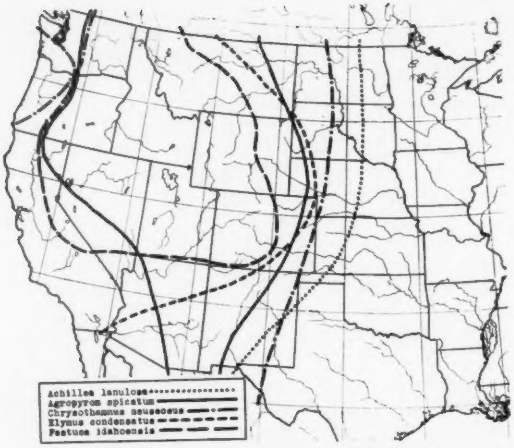

FIG. 19. Ranges of five species selected as the most important indigenous species which are well represented in two or more zones, and which extend practically across the entire unforested area north of the Blue Mountains.

ECOLOGICAL AFFINITIES

PALOUSE GRASSLANDS

One of the most outstanding ecological characteristics of the Palouse grasslands is the periodicity of the vegetation which is intimately tied up with the preponderance of winter precipitation and the mildness of temperatures at that season. These characteristics of climate and vegetation contrast sharply with all North American grasslands east and south of the Northern Rockies. However, the prairie region of the San Joaquin-Sacramento Valley in California has a climatic pattern very similar to that of the Palouse, and the original prairie cover of this valley was similar to the Palouse in the stature and periodicity of the dominants. The dominant and most of the subdominant plants of the California prairie as described by Clements (Clements and Shelford, 1939) were nevertheless entirely distinct from those of the Palouse prairies as described in this paper.

The climate of the west coast of the United States is characterized by (1) mild temperatures, and (2) dry summers. The California prairie receives a good measure of these characteristics since it is separated from the ocean by only the low coastal ranges. The Palouse region is situated somewhat farther inland and to the lee of much higher mountains, but the winds of a well-developed storm track in this latitude blow steadily from the Pacific Ocean extending some features of the coastal climate far inland over Washington, northern Idaho, and western Montana. The tendency for less than half the annual precipitation to fall in summer, and for winter temperatures to be somewhat mild is very noticeable as far east as the Bitterroots. East of the Bitterroots the coastal influence is very weak, and east of the continental divide a strictly continental climate prevails.

Over this inland extension of the coastal climate, from the divide of the Cascades to the divide of the Rockies, and from southern British Columbia to the southern end of the Bitterroots, occur grasslands of the Palouse type. The Agropyronetum, or communities very similar to it, occurs at suitable elevations over this entire peninsula of coastal climate, even where the oceanic influence is very weak as in western Montana. The Festucetum is much less widely distributed. So far as the writer is aware, it is limited in extent to two narrow belts, one of which borders the lower timberline along the west (windward) edge of the Blue Mountains,[12] and the other occupying an identical position along the west edge of the Bitterroots from Spokane to the vicinity of Whitebird, Idaho. Because of the restricted ranges of important species, typical stands of this community can only occur within this region.

This grassland province centering about the Bitterroots is to be looked upon as floristically distinct from all other grasslands, but possessing a single ecological character (type of periodicity) in common with the California prairies.

ARTEMISIA-AGROPYRON ZONE

The Artemisietum and halophytic communities of southeastern Washington are continuous (between the Blue and Cascade Mountains) with nearly identical vegetation in the intermountain region (Pickford, 1932) from which they are obviously derived.

SUMMARY

That portion of the Columbia Plateau which includes approximately the southeastern quarter of Washington has not been forested since the elevation of the Cascade Mountains during Pleiocene time. With the resultant development of aridity the driest portion of this area became inhabited with desert-like communities of species which immigrated chiefly from the south, while in less arid portions of the area there developed the "Palouse" grasslands which contain a high proportion of more or less endemic species.

This modern vegetation may be divided on the basis of climatic climaxes into three zones: the Artemisia-Agropyron zone in the western, driest part of the area, the Agropyron-Poa zone in the intermediate, less arid region, and the Festuca-Agropyron zone along the eastern, most mesic edge of the Plateau. These vegetation zones are closely correlated with major soil series.

Most of the detailed vegetational analyses concern the two prairie climatic climaxes. The Agropyron-Poa association is dominated by grasses of the bunch habit, is vegetatively active in the cool, rainy winter and spring, but remains completely dormant during the hot dry summer. The Festuca-Agropyron association is dominated by perennial forbs, is floristically richer than the other prairie, and has a shorter period of aestivation.

The principal edaphic, fire, and biotic climaxes of all three zones are briefly described.

[12] The writer has observed this zone as far south along the Blue Mountains as the latitude of Pendleton, Oregon.

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PLANT ECOLOGY OF THE COASTAL SALT MARSHLANDS OF SAN DIEGO COUNTY, CALIFORNIA

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PLANT ECOLOGY OF THE COASTAL SALT MARSHLANDS OF SAN DIEGO COUNTY, CALIFORNIA

INTRODUCTION

The purpose of this work was to determine and record the distribution of salt marsh plants in San Diego County, to consider the environmental conditions under which they grow, and to study the characteristics of the principal genera under these habitat conditions. No published literature on salt marshes of this area has been found.

The tidal or salt marshlands of San Diego County cover about 32,000 acres along the coast from the Mexican boundary to Orange County. These areas are separated from each other by higher lands, principally mesa lands, the marshlands occurring along the shores of bays or at the mouths of rivers.

Figure 1 gives a delineation of the coastal areas and the marshlands. Twelve stations, numbered from south to north, were selected for special study. In addition, there is about an acre of marshland plants at Canyon de las Encinas between stations 7 and 8, but, as no stream flows through it and as it is much smaller than the other areas, it was disregarded. North of the farthest station, the Santa Marguerita, the coast rises; and, although there are six canyons between it and the northern limit of the county, some with small areas of marsh plants, these were not important enough to be included in the studies.

The marshlands have been formed in several ways. The littoral current sweeping down the coast from north to south has thrown up sand at the mouths of valleys. This has blown inland to form sand spits separating the lower end of the valley from the ocean or even cutting off the stream except during storms. In some cases it has formed a series of small dunes partially separating the bodies of water from the ocean, as in the case of San Diego Bay. In addition the silt from the rivers which flow at times into the marshlands has built up portions where vegetation can get a start.

The extreme range between low water, —1.8 feet, and flood tide, 7.7 feet, in January, 1939, was 9.5 feet. In July of the same year it was 8.1 feet. The extreme range between low water, —1.7 feet, and high water, 7.5 feet, in November, 1940, was 9.2 feet.

The field work extending over a period of nearly three years was started in September, 1938. After a reconnaissance survey, monthly trips were made to all areas. On these trips, a preliminary survey of the areas was made; the stations were located, and the relative size of the areas, the abundance and distribution of the species and their relative importance were determined. On the monthly trips samples were taken for the determination of the salinity of the soil and water, the tide level was measured, the influence of drainage and tides was noted, the general growth conditions of each species and its time of flowering were observed. On each trip one station was selected to be studied in greater detail.

FIG. 1. Showing location of twelve stations where studies were made.

The water samples were obtained by dipping a glass container into the saline water and immediately corking. The soil samples were obtained by digging, allowing the water in the hole to settle. All the water and soil analyses for salinity were made by the Scripps Institution of Oceanography, La Jolla, through the kindness of Dr. E. G. Moberg. The Natural History Museum, San Diego, supplied the list of mollusks and crustaceans.

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PLANT ECOLOGY OF THE COASTAL SALT MARSHLANDS OF SAN DIEGO COUNTY, CALIFORNIA

INTRODUCTION

The purpose of this work was to determine and record the distribution of salt marsh plants in San Diego County, to consider the environmental conditions under which they grow, and to study the characteristics of the principal genera under these habitat conditions. No published literature on salt marshes of this area has been found.

The tidal or salt marshlands of San Diego County cover about 32,000 acres along the coast from the Mexican boundary to Orange County. These areas are separated from each other by higher lands, principally mesa lands, the marshlands occurring along the shores of bays or at the mouths of rivers.

Figure 1 gives a delineation of the coastal areas and the marshlands. Twelve stations, numbered from south to north, were selected for special study. In addition, there is about an acre of marshland plants at Canyon de las Encinas between stations 7 and 8, but, as no stream flows through it and as it is much smaller than the other areas, it was disregarded. North of the farthest station, the Santa Marguerita, the coast rises; and, although there are six canyons between it and the northern limit of the county, some with small areas of marsh plants, these were not important enough to be included in the studies.

The marshlands have been formed in several ways. The littoral current sweeping down the coast from north to south has thrown up sand at the mouths of valleys. This has blown inland to form sand spits separating the lower end of the valley from the ocean or even cutting off the stream except during storms. In some cases it has formed a series of small dunes partially separating the bodies of water from the ocean, as in the case of San Diego Bay. In addition the silt from the rivers which flow at times into the marshlands has built up portions where vegetation can get a start.

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STATIONS

The twelve stations from the Mexican boundary northward are as follows:

1. Tijuana.
2. San Diego.
3. Mission or False Bay.
4. Soledad (north of Torrey Pines).
5. Del Mar.
6. San Elijo.
7. Batiquitos (at the mouth of the San Marcos Creek).
8. Aqua Hedionda.
9. Buena Vista.
10. Loma Alta.
11. San Luis Rey.
12. Santa Marguerita.

1. *The Tijuana River* slough extends parallel with the coast line from the international boundary northward to Imperial Beach. It has been formed by a ridge of sand dunes built up just east of the beach area. This prevents the water of the slough from emptying into the ocean except at one portion. In addition, this area has been built up by silting from the Tijuana River. It is a good area for study, as it is largely undisturbed by human activity.

During the high tides it is greatly flooded and appears as a large expanse of water, but in summer the water is confined to small anastomosing channels of sluggish water. The soil is all heavy gray clay except on its western margin, where the sand from the spit has been blown over into the slough. The stream has cut deeply (about two to three feet) into this spit near the mouth. In winter, high-tide storms flow over the entire length of the spit into the slough and carry in debris over a stretch of several miles. On the whole, the area covered by marsh plants is more extensive than the open water. No craft larger than rowboats can be floated.

Of the plants, Salicornia is the most abundant, with *S. pacifica* in pure stands at the lower edges while at higher levels associated with Distichlis, and where still higher with Distichlis and Frankenia. In addition, the conspicuous plants are Spartina (in water), Atriplex, Monanthochloe, Suaeda, Limonium, Batis, and Cordylanthus, where the land is drier. There is no vegetation on the area around the channel where water discharges into the ocean through a sharply cut sand bank.

2. *San Diego.* The San Diego Bay area has marshlands around the edges of the bay where man has not as yet dredged, filled, made docks, put in fishing canneries, salt works, or other improvements. The salt marsh is but a minor part of the bay region, being relegated to small areas along the east and south shore lines and to a strip on the west bordering the Silver Strand, a sand spit extending southward from Coronado, and separating the bay from the ocean.

The margins of the bay have little shallow water; the water in much of the bay can accommodate navy ships, ferries and other craft. It is always open to

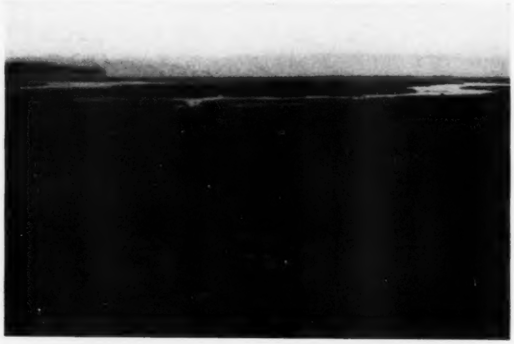

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FIG. 2. A. Tijuana slough (station 1), just above the Mexican border, showing meandering stream with zoned vegetation in foreground.

B. Mission Bay (station 3), east shore, showing large expanse of water with Spartina in foreground.

the ocean through a wide channel. Vegetation along the east and south end of the bay grows mostly in silt, on the west side in sand. The Sweetwater and Otay rivers and several canyons drain into the bay on the east side.

Much debris, including kelps, is washed in during the winter storms. There is present considerable Spartina and Salicornia; and as one goes to higher ground much Limonium, and in addition, Suaeda, Atriplex, Frankenia, Monanthochloe, Distichlis, Cordylanthus, and on still higher ground Lotus and Aplopappus. Batis spreads on wide, flat, damp places. Ulva is abundant in water along the sandy portion of the shore line.

3. *Mission or False Bay.* This bay is much shallower than San Diego Bay and is now in the process of being partially drained. Government work of drainage consists in digging channels in straight lines down to the open water and piling the excavated material in conical mounds along the sides of the ditches. This aids in draining low lands and controlling mosquitoes. Much of the area is covered with water too deep for vegetation, principally the

north end, which is navigable for small craft. The southeast and south sides (nearest to the city of San Diego) formerly had hundreds of acres of marsh, which as a result of drainage is gradually becoming too dry for marsh plants and is now being laid out into building lots, race tracks, landing fields, and army encampments.

Formerly the San Diego River emptied into San Diego Bay; and a large low flat existed between Mission Bay and San Diego Bay, the river taking first one course across it and then another. A channel was built to confine the river, which now flows directly west and empties into Mission Bay. The low lands over which it once flowed have all been reclaimed. The undeveloped areas of the bay are a bird sanctuary.

In the north end of the bay are large islands of Spartina which look like great fields of wheat in the summer. Spartina is more abundant here than at any of the other stations. This is due to the depth of the water, being too deep in most places for any other marsh plants. It is frequently in pure stands or sometimes associated with a small amount of *Salicornia pacifica*. On the shallow, flat end of the bay there are present Salicornia, Suaeda, Distichlis, Monanthochloe, Limonium, and Atriplex, and on higher and drier spots Aplopappus and Atriplex are abundant. Frankenia and *Salicornia subterminalis* are establishing themselves on the artificially placed mounds of clay made in digging drainage channels. Along the edges of the ditches where aeration is better there is always abundant vegetation, but there are many acres which are bare of vegetation and are covered with a glistening layer of salt. Where drainage is present, either artificial, or natural, and aeration is improved, Salicornia appears. It is most luxuriant on the edges of the drainage channels. It is green, tall, and hardy in appearance.

4. *Soledad Station.* This marshland, north of Torrey Pines Preserve, extending in a southeasterly direction, lies in the flat, wide river valley of the Soledad with a spur into McGonigle Valley. At its northwest end it connects with the ocean during portions of the year. Within its area are numerous narrow anastomosing channels connecting with several wide, shallow bodies of water, which, during the summer, generally become dry. It is mostly marshland with little open water.

The marshland has been formed by the sand spit across the valley preventing the sea water from flowing into the area, except at one end. In addition, its shallowness is in part due to the silt which has been brought down by the creeks during the rainy season. The soil is fine gray silt, except at the seashore, where the wind has blown in sand. This station is much less disturbed by man than the two preceding.

The flat areas which make up considerable portions of the marsh lie too far below water during the winter to support vegetation, and, during the summer, are too dry for vegetation to become established. They lie dry, bare and cracked in the summer except for a covering of algae, which in late spring is green and by July becomes yellow-brown. Raised islands above these flats support large amounts of Salicornia, which appears as either pure or mixed colonies. Where there is a water channel, Spartina growing along it is noticeably more luxuriant than elsewhere. It is frequently twice as tall, greener and stiffer, less subject to being matted and becoming blown down and flattened. In the flats Salicornia grows in almost pure stands. On the hillocks it is luxuriant, on the low portions poor. As the water recedes in the summer, algae are left matted on the lower branches of the Salicornia plants. Cuscuta grows on Salicornia in abundance. In higher, drier spots above Salicornia are Heliotropium, Aplopappus, and Atriplex. The upper edges of the marsh run into pasture land, with Cyperus, Typha, and Rumex most frequent.

5. *Del Mar Station.* Located north of Del Mar at the lower end of the San Dieguito River Valley, this salt marsh has been closed off from the ocean by a sand spit except for a channel which the stream has cut through it at its north end. Here the stream has been confined to a more or less definite channel, though on one occasion during the rainy season it broke its bounds and carried away the north approach to the highway bridge. During the summer the channel to the ocean is usually dry.

This area is almost as wide as long, but there is little real marshland now left, as most of it has been laid out in County Fair grounds, the Del Mar Racing tracks and, in addition, many acres of parking space. One portion of the valley bottom is used for making adobe bricks. To prepare this area, considerable dredging has been carried on, which has deepened and straightened the river channel. Sand has blown in also. Farms have been developed along the north and east edges of the marsh. Moreover, the marshland is crossed by a railroad and two highways, one of which is laid principally on the inner edge of the sand spit. Since there is little of the area which has not been disturbed, of all the stations it now contains the smallest number of plants.

Salicornia, Distichlis, and Monanthochloe are present as well as those plants which are found on higher ground as Cressa, Spergularia, and Aplopappus. Along the north edge of the marshland is a considerable development of Typha, showing a transition from salt marsh to fresh-water swamp. This is due to the fresh water which seeps down from the irrigated districts. Salinity of the water was shown to be 0.86 in parts per thousand. The abundance of Frankenia here shows that it is not a salt obligate.

6. *San Elijo.* Between Encinitas and Solana Beach there is a lagoon formed by the sand dunes at the mouth of the San Elijo Valley. It is a relatively small area about four times as long as wide, extending northeastward with little open water, particularly in summer. It has not been disturbed except for a railroad crossing it and to some extent by the raising of the highway which passes along its west side. The small stream empties into the ocean through a channel it has cut at the north end of the valley.

Along the west edge the soil is sandy, as it has been blown in from the beach. The east edge is silt. On the higher ground one finds Lotus, Juncus, Jaumea, Heliotropium, Limonium, Frankenia, Monanthochloe, and Distichlis. Lower are several species of Salicornia, with *S. subterminalis* making large islands.

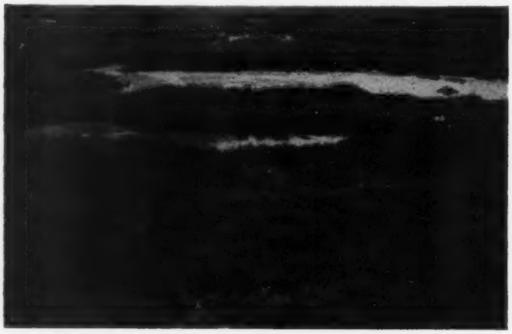

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FIG. 3. A. San Elijo Lagoon (station 6), in low water with Salicornia in the foreground.

B. Buena Vista Lagoon (station 9), with clumps of Juncus at the right.

7. *Batiquitos.* At the mouth of the San Marcos Creek north of Leucadia is the Batiquitos Lagoon, larger than the preceding area. Extending directly east and west, it is about six times longer than wide. The lagoon has been formed by sand dunes along the coast closing the mouth of the valley. The dunes are continually invading the marsh in spite of the highway which has been built across the lagoon from north to south. At low tide the stream channel is seen under the railroad tracks which cross from north to south several hundred feet east of the highway and then the stream makes a big loop and passes under the highway bridge, emptying into the ocean through a small channel which becomes clogged with sand when the water course is low, there being no connection with the ocean during dry periods. When the tide is low, large mounds of rounded stones about three inches in diameter are exposed.

The principal genus is Salicornia. In the middle of the area on higher ground are considerable Distichlis and representatives of a number of other marsh genera, with Salicornia by far the most abundant. A small amount of Ulva is seen.

8. *Aqua Hedionda.* The flow of the Aqua Hedionda Creek is not extensive. The marshland is formed by silting at the mouth of the valley, which extends in an easterly direction about six times longer than wide. The connection with the ocean is made only during storm and high tides. During the months of low tide it was noticed that there was an extensive deposit of gravel with large rounded stones on the surface of portions of the marsh. It appears to be the same type as that washed up on the strand. The area is undisturbed except for the railroad and highway crossings and for a small road spur into the marsh. Some of the land on the outer edge of the marsh has been farmed. Many wading birds frequent this area. A large island supports *Salicornia* spp. which are especially abundant on its edges. Other representatives of the marshlands are Atriplex, Limonium, Suaeda, Heliotropium, Frankenia, Monanthochloe, and Distichlis.

9. *Buena Vista.* North of Carlsbad the Buena Vista Creek has formed a wide valley, the upper end with a lagoon, the lower with marshland. During the summer the creek from the lagoon is too meager to connect with the marshland, but in winter the surrounding areas drain into the creek which overflows and the entire marshland may be under several feet of water. The area is crossed by a railroad track and two highways. The marsh is cut off by low-lying sand dunes from the ocean except at very high tides. The marsh extends in a northeast and easterly direction, six to seven times longer than broad. The creek channel lies in the center of the valley with the lower stretches of marsh covered by water in winter. In summer the channel only is partly filled with water, the rest of the marshland consisting of large, flat salt-covered areas without vegetation. The area is a bird sanctuary.

Salicornia is the most abundant genus in the lower areas, while Frankenia is more frequently found in the upper, slightly raised places of the river valley. Cressa, Heliotropium and Distichlis are also fairly common, while Typha and Scirpus have established compact colonies on the edges of the marsh. On the islands which are raised above the salt flat there is mostly Salicornia, which grows very luxuriantly, but where it has migrated to the salt flat, its growth is meager. Some bare spots are abundantly covered with algae in the spring. In the marshland above the highway which crosses at its upper end Atriplex, Aplopappus, and Cotula are present. Here there is more seepage of fresh water and the percentage of salinity is low. As one ascends the lagoon area Cyperus, Typha, and others come in, while Frankenia appears where cattle and horses pasture.

10. *Loma Alta.* Loma Alta lies between South Oceanside and Oceanside in the valley made by the creek. Loma Alta Creek follows a narrow channel about 20 feet wide in the center of the valley, which is silted at the shoreline and rarely connects with the ocean. There is little open water. The marshland extends in a northeasterly direction and is traversed by two highways and one railroad. The valley is quite flat with its lower end salt-covered and mostly without vegetation. In some places it has summer mud flats. During the winter season the mud flats are covered with water which does not permit any plants to gain a foothold. The principal saline species are represented. Where there is a slight rise in ground the vegetation is abundant, especially with Salicornia. On the sides of the valley, where the ground is raised above the salt level for most of the year, large clumps of Typha are present. At the upper edges of the marsh Typha and Frankenia are abundant.

11. *San Luis Rey* (north of Oceanside). At one time the wide and flat San Luis Rey River Valley, extending many miles inland, was mostly marshland, but now for miles orange groves and farm lands have been developed. The water is now pumped from the river bed to such an extent that it does not flow extensively as it did formerly, except during and after a heavy rainstorm. The marshlands, such as still persist, are found along the margins of the valley near its lower edges, and groups of marsh plants are often intercepted by areas of fresh-water plants as the seepage from the irrigated districts passes seaward. This interplay of salt- and fresh-water areas in this section is most interesting, for it is never permanently located, changing with the seasons. During very high tides there is an influx of salt water; varying between these are times when the tides are low or high and when rains may come and when irrigation increases or decreases. The area has been disturbed by roads, a railroad and orchard and farm lands.

Islands with or without vegetation appear in the center of the slowly moving stream, the channels of which are but a few feet wide. On nearing the ocean, the passage of the stream is obstructed except during high tides by a ridge of low sand dunes. A marsh is formed behind these dunes. On the outer and upper edges of the marshlands Cyperus, Typha, and Sausevaria fill low spots. Atriplex, Frankenia, Distichlis, and Jaumea are also common. In addition, there are small islands of Typha. There is no indication of salt on the surface as at some of the other stations. At the ocean, the marshland supports considerable Salicornia.

12. *Santa Marguerita* (north of Oceanside). This is the station farthest north, a short distance north of the San Luis Rey River. This marshland has been formed in the lower portions of the Santa Marguerita River Valley by sand dunes which have built up a barrier across the mouth of this wide valley. The broad stream passes through this low area, emptying into the ocean throughout the year. The area is cut across by both a highway and a railroad and has been disturbed at its south end by the development of a landing field. This field is so low that it is frequently inundated by heavy rains and storm tides. On the upper edges of the marsh are Atriplex and a fairly well represented number of saline genera. Lower, an abundance of Salicornia dominates the area. Along the edges of the stream the flow of water prevents the development of much vegetation.

ENVIRONMENT

The various habitat factors have been studied and an attempt made to discover the factors that are effective in determining the distribution of each plant or group of plants.

CLIMATE

The areas under investigation are situated in the foggy desert belt according to Russell (1931). The nature of the climate is indicated in Table 1, with data supplied by the Weather Bureau, U. S. Department of Agriculture, San Diego.

TABLE 1. Climatic conditions during 1938-40 and averages.

Year	Temperature (mean annual)	Temperature (maximum and minimum)	Mean relative humidity (percent)	Total precipitation in inches	Sunshine (percent)	Wind direction, average hourly velocity in miles
1938......	62.2	88 42	72	13.01	68	N.W. 6.7
1939......	62.9	106 36	72	9.97	67	N.W. 6.5
1940......	63.6	95 41	73	14.75	65	W. 6.7
Average...	62.9	highest 106 lowest 36	72	12.58	67	N.W. 6.6

TEMPERATURE OF AIR AND SOIL

The maximum air temperature during the time of investigation was 106° F.; the minimum 36° F., with no killing frost, and the average about 71° F. The relative humidity is about 72 percent, the average for the past three years. The coast is subject to some fog, but has an average of 67 percent of sunshine.

The average soil and water temperatures taken at 10 cm. depth at each of the twelve stations during a year's period show a slight range from 14° to 27° C. A ten-centimeter depth was selected, as the largest number of roots are found at this depth. A hole was made in the mud in a Salicornia association at each station and the thermometer thrust into the water which seeped in. Except in January and February, water temperatures during the morning hours (when checking was made) showed not more than 2 to 3 degrees higher than soil temperatures at the same station during the same time. On any given day when readings were made, there was only a slight range, about 6 degrees, throughout the stations. Figure 4 gives the averages of water temperatures in the lagoons and in the soil during one year.

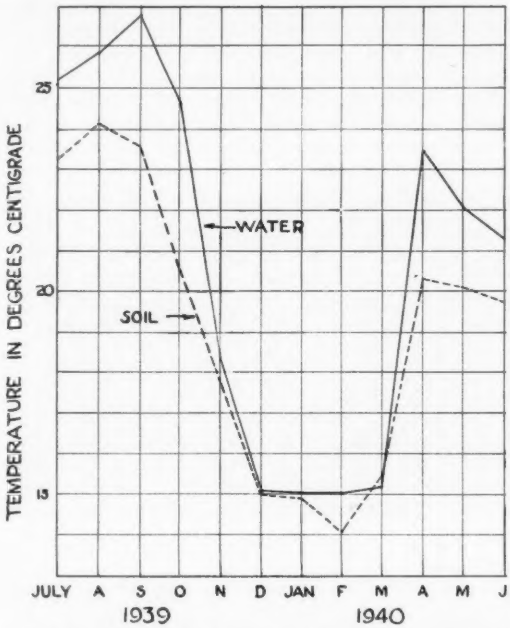


FIG. 4. Average temperatures of water in lagoons and in soil, taken at 10 cm. depth (average of twelve stations). Readings 8:30 a.m. to 12 noon.

Water temperatures are uniform on the shores of the larger bodies of water, rising in the summer and early fall. The water temperature in small anastomosing bodies of water which have been cut off from the ocean was 6.5° C. higher at 10 A.M., October 21, 1939, than the main body of water which connects with the ocean. The lowest water temperature during field excursions was 11° C., and the highest 32° C. Temperature plays but a small part in the distribution of salt plants throughout the area. As the species are fairly uniformly distributed throughout the twelve stations, temperature is, therefore, not considered a determining factor in the distribution of plants within the area, although it does determine, no doubt, the kinds of species present as compared with another area, as in the state of Washington or New Jersey, for instance.

SALINITY OF WATER AND SOIL

Water salinity is dependent on (1) connection with ocean, (2) height of the tide, (3) elevation of the marshland, (4) precipitation, (5) discharge from rivers or streams, (6) irrigation seepage, and (7) evaporation.

Some of the stations are always connected with the ocean, some during high tides, and others only during storm tides. San Diego Bay (station 2) and Mission Bay (station 3) are always connected with the ocean by deep, wide channels; Santa Marguerita (station 12) connects with a low channel. Tijuana (station 1) is open to the ocean at high tides; Soledad (station 4) to storm tides. Those not regularly connected with the ocean have an increase in salinity during the summer months as a result of the increased evaporation and the lack of precipitation, in addition, of course, to the absence of a fresh supply of water from the ocean. The upper edges of some of the marshlands such as Soledad, Del Mar, and Buena Vista, having been gradually raised by silt from the nearby hills, little tide water reaches them and the percentage of salinity is low.

In Figure 5, the salinity of the water at the twelve stations from January, 1939, until June, 1940, is given. A general trend can be seen in the percentage of salinity as the winter rains cease in most of the stations. For example, at Tijuana (station 1), San Diego (station 2), and Mission Bay (station 3) where there are large areas of water, there is on the whole a gradual increase in salinity from the winter months into the summer, and with rains in September a noticeable decrease. River valleys such as San Luis Rey (station 11) and Santa Marguerita (station 12) through which streams flow in the winter show little salinity at that time. The Santa Marguerita increased from a salinity in parts per thousand of 0.31, in January, 1939, to 34.60 in July of that year. Fluctuation is greater at these stations than in large bodies as San Diego (station 2) or Mission Bay (station 3).

A few stations in the dry summer months have a decrease in salinity, where, on the whole, might be expected an increase. Such is the case at Aqua Hedionda (station 8) where fresh-water seepage from irrigation decreases the amounts of salinity during certain periods. From June to September, the driest months, at San Elijo (station 6), and Loma Alta (station 10), the increase in salinity was exceedingly great, far above that of the other stations. The two stations do not receive flushing by tides during the summer months nor seepage from fresh-water sources. The bodies of water are shallow and are subject during these months to considerable evaporation. These factors determine the excessive salinity. In large bodies of water, the water samples taken in the open water along the shore at various points indicate that there is not more than 0.30 parts per thousand variation in the salinity. Large bodies of water have less salinity than small bodies near them. In June, 1939, San Diego Bay had a salinity of 35.60 parts per thousand, while a small pool 100 feet from the shore had 40.39. In August of the same year, the bay had 37.61, while the pool had 42.52. Evaporation from small bodies of water without replacement of water makes this difference.

Soil salinity is dependent on (1) the height of the tide, (2) the elevation of the marshland, (3) the proximity to ocean, creeks, or ditches, (4) water from precipitation, streams, creeks, and irrigation, (5) depth in the substratum, and (6) evaporation. The height of tides influences the salinity of the soil. In the upper stretches of the marsh area where high or storm tides occasionally leave salts, there is much less salinity than in areas flooded daily. The upper edges

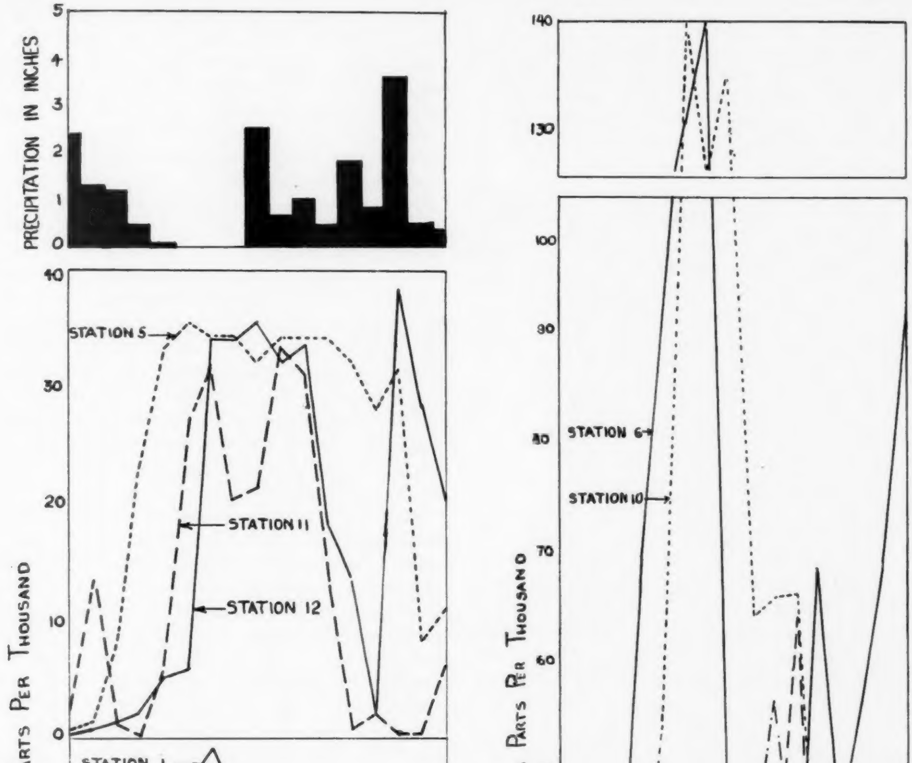


FIG. 5. Salinity of water (in parts per thousand) at twelve stations taken monthly and precipitation in inches from January, 1939 until June, 1940.

of the marshland have silt brought down by rains, and with gradual fill there is less salinity.

Figure 6 shows the salinity of the soil water taken at 10 cm. depth from places as identical as possible at each of the twelve stations. The record is from January, 1939, until June, 1940. A general increase in salinity is seen during the summer months at most of the stations.

When a body of water connects with the ocean, the salinity of the soil near it is about 2.0 to 3.0 parts per thousand lower than in areas surrounding bodies of water not recently connected with the ocean. The soil around large bodies of salt water shows greater uniformity in salt content throughout the year than around smaller bodies of water. As the water recedes in summer and the marsh is cut off from the ocean, a white crust appears over large areas as at stations six and ten. The salinity in this soil is great, reading up to 234.23 parts per thousand. Areas half as high in salinity do not support any plants.

Soils around San Luis Rey (station 11) with a sharp decrease in salinity during July when there was no precipitation, show the effect of fresh-water drainage from above. Soils around Aqua Hedionda (station 8) show slight increase in salinity from April to December, 1939, although so much water from the creek flooded the marshland in April it was difficult to get soil samples. The salinity of the soil decreased from 21.60 parts per thousand in February to 1.91 in April as the spring freshets emptied into the marsh.

Salinity increases with soil depth, as these two examples show. At Soledad station in April, 1939, at 10 cm. salinity in parts per thousand was 7.92; at 20 cm., 8.96; at 30 cm., 9.45; at Batiquitos station at 10 cm., 27.75; at 20 cm., 27.92; at 30 cm., 28.37.

Evaporation of the moisture from the soil causes a precipitation of salts, which form a white crust on the soil surface. It is with difficulty that plants can succeed because of the salinity produced, ranging up to 173.61 parts per thousand at Loma Alta (station 10) and 234.23 at San Elijo Lagoon (station 6).

WATER—TIDES, WATER TABLE, RAINFALL, STREAMS, AND IRRIGATION

Tides are a major factor, responsible for the presence of marsh vegetation. They control the vertical distribution of the species and affect the location of the various species by the number of submergences at high levels and through the number of exposures at low tides. While there were actually 37 days of high tides, in which the tides rose to 7 feet or more during 1939, only 17 of those occurred during the active growing season. The highest tide of the year was 7.7 feet in January, with five tides at 7 feet or over in that month, four in February, three in June, five in July, four in August, two in September, three in October, four in November, and seven in December. All of these highs came in the evening or before 9:53 in the morning. Although those tides rose high above the normal limits, they did not completely inundate any species except Spartina and Salicornia. Distichlis, Frankenia, and others were only partly submerged. From debris left, it can be seen that all salt marsh species may be covered with salt water for a short period when winter storms and high tides coincide. Tidal trash is found even above the upper limit of Cordylanthus, Limonium, Atriplex, and other species seldom submerged.

It must be remembered that the water levels keep changing from high to low twice daily, making a continued submergence and exposure of all the plants below the high-tide marks. All plants at lower levels have their leaves and stems covered, while those of the upper levels are affected by being submerged only during very high tides. This repeated ebb and flow of salt water restricts the supply of oxygen to the upper parts of the plants and shuts it off from the lower parts. Sand spits serve to reduce greatly the height of the tides within the areas, although storm tides frequently flow over the entire spit, as at Tijuana (station 1).

The water table is influenced by daily tide movements and by spring and neap cycles. The water table is continually varying. It is determined by (1) height of the tide, (2) height of any given area in the marsh, (3) height of previous tide, (4) distance from the ocean, (5) size of channel, (6) velocity and direction of wind, (7) dune action at outlet to ocean, (8) precipitation, (9) flow of streams and creeks, (10) irrigation, and (11) evaporation.

The movement of water in the substratum takes place through lateral seepage, and by capillarity and evaporation. The lateral seepage may be saline from tidal basins and creeks or fresh water from streams and from irrigation seepage. It is increased by the proximity to the water channel, the wider the channel the greater the increase. Capillarity brings water to the surface where it is evaporated. Wind velocity, averaging about 6 to 7 miles per hour, is so low that it exerts little influence. Water is also raised from the soil by plants. Taylor (1938) believes that the under-surface water may well be the explanation of the continuity of the marshes as a plant society.

In Table 1 is given the precipitation for each year during which the study was made. Most of the rain comes, in this part of the country, from November to May. It is meager, of course, compared to that received in marsh areas on our northwest coast or along our eastern shores.

At each station one or more streams or creeks flow through the area, at least for a part of the year, usually for a week or two after a heavy rain. Santa Marguerita and San Luis Rey have the largest flow. They do not compare, however, with other sections of the country which have a steady and large flow of water throughout the year.

Irrigation in a number of river valleys causes a seepage of fresh water to come to the marsh areas below them, somewhat decreasing the salinity, especially in the smaller areas.

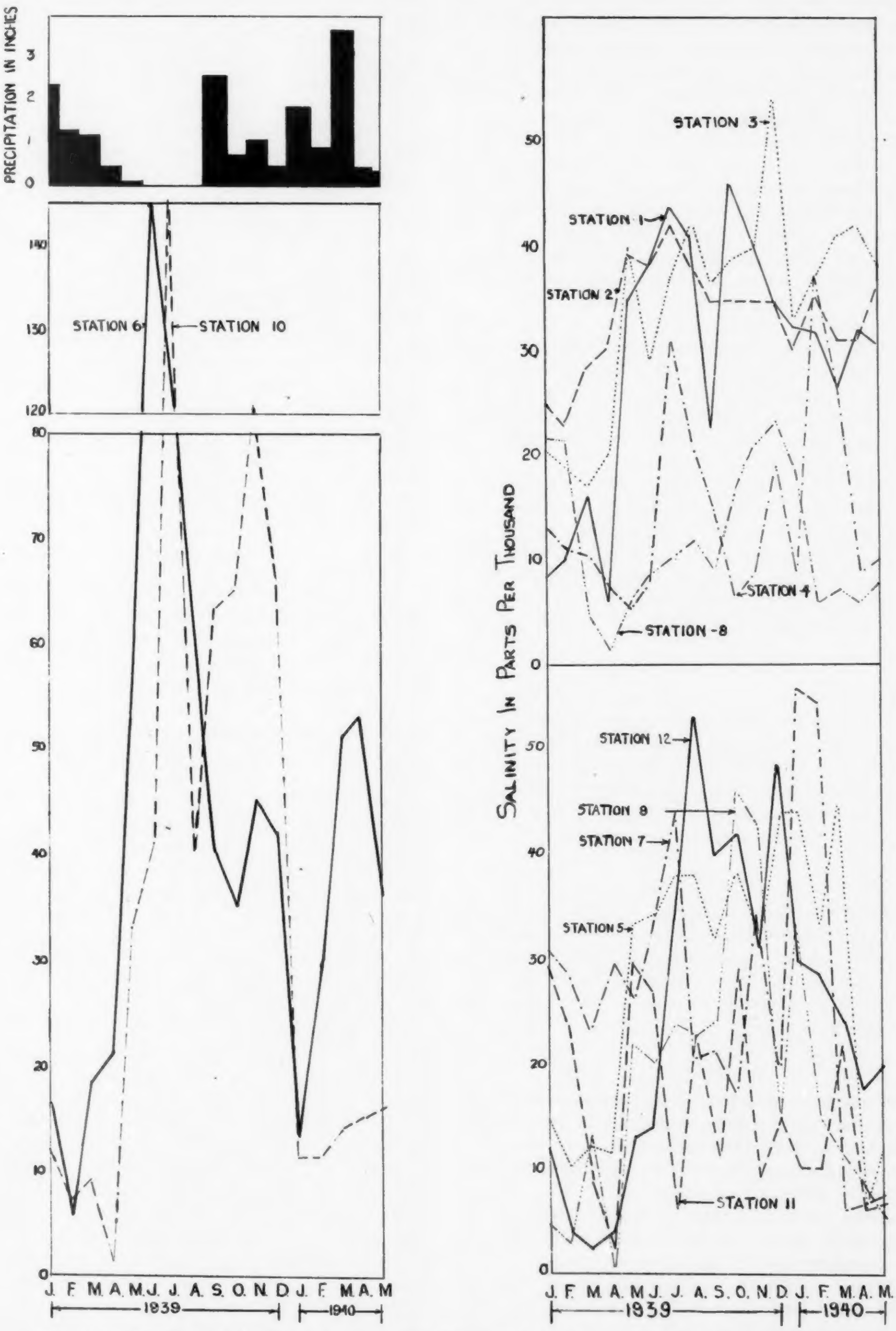


FIG. 6. Salinity of soil water (in parts per thousand) at 10 cm. depth at twelve stations taken monthly and precipitation in inches from January, 1939 until June, 1940.

Aeration of Soil

The subterranean aeration of the soil is important in determining the vertical location of species, as even a slight rise of land admits improved aeration. The vertical distribution of species is determined principally by drainage, which improves aeration, and salinity.

It is seen that when aeration is improved plants which were not represented previously invade this area. On a mud flat, vegetation will cover the area except where small depressions are present. At the San Elijo Lagoon and others, a thick crust of decomposing algae forms on the bare ground as the water dries up. No living plants are present.

The effect of improved aeration is seen where ditches and channels have been dug. Along the edges of the channels a luxuriant vegetation of marsh plants appears as compared with the low, flat areas back from the channels. On mounds left from digging, the ground having been turned over and aeration improved, plants have taken immediate possession.

Animals play a minor part in increasing aeration by burrowing. Shells of several species are widely scattered on the mud flats. If a pole is thrust into the mud and quickly removed, bubbles of air arise from the hole thus made, or numerous bubbles arise through the mud at various points as far away as a foot from the pole.

Light

Light is intense. There are many sunshiny days, although both high and low fog are occasionally encountered along the coast, especially in the mornings. The reflection from the water is considerable so that plants receive both direct and reflected light. The small plants are hardly protected by others, as all of them are low-growing.

Evaporation

Evaporation in these coastal areas is reduced by both high and low fogs. Evaporation readings of Livingston white porous cup atmometers near the upper edge of the marsh showed a range from 45 to 130 cc. per week over a period of four months from September to January.

Biota

Man has wrought many changes in the areas. Extensive drainage has been carried on at Mission Bay for homesites, landing fields, and race tracks. Salt works, fish canneries, and other commercial activities are present around San Diego Bay. At a number of stations where the salinity is low, ranching and pasture lands have been developed. Birds are particularly numerous in the areas designated as bird sanctuaries. Mollusks and crustaceans of the salt marshes and mud flats aid in aerating the soil. The mollusks are *Truncatella californica* Pfeiffer (California Looping-snail), *Truncatella stimpsoni* Stearns (Stimpson's Looping-snail), *Cerithidea californica* Haldeman (California Horn-shell), *Cerithidea californica hyporhysa* Berry (Smooth Horn-shell), *Melampus olivaceus* Carpenter (Olive Ear-shell), *Bulla gouldiana* Pilsbry (Gould's Bubble-shell), *Conus californicus* Hinds (California Cone), *Phasianella compta* Gould (Pheasant-shell), *Nassarius tegula* Reeve (Covered Basket-shell), *Polinices recluziana* Deshayes (Southern Moon-snail), *Acmaea paleacea* Gould (Chaffy Limpet), and *Acmaea depicta* Hinds (Painted Limpet). The crustaceans are *Orchestia traskiana* Stimpson (Marsh Amphipod), *Sphaeroma pentodon* Richardson (Boring Isopod), *Upogebia pugettensis* (Dana) (Ghost Shrimp), *Callianassa californiensis* Dana (Ghost Shrimp), *Callianassa longimana* Stimpson (Ghost Shrimp), *Portunus xantusii* (Stimpson) (Swimming Crab), *Speocarcinus californiensis* (Lockington) (Burrowing Crab), *Hemigrapsus oregonensis* (Dana) (Mud Crab), *Uca crenulata* (Lockington) (Fiddler Crab), and *Uca musica* Rathbun (Fiddler Crab).

Plants exert a decided influence on each other. Those in the upper stretches of the marsh, where salinity is less and growing conditions more favorable, prevent species from the lower, wetter portions from getting a foothold.

Summary

The climate is favorable for plant growth because of its evenness and lack of frost. The salinity remains almost constant in and around the large bodies of water, and decreases at all stations in winter and early spring as rainfall acts as a depressant upon the surface saline concentration. The exception appears where streams or irrigation augment the fresh-water supply during other portions of the year.

As there is a fluctuation in the salinity of the soil in the different plant communities throughout the year, there is a general range within this for each plant community. The maximal values in any given community or the average total concentration for the year may be the deciding factor for the presence of a certain community. It may be that aeration plays an important part, rather than the maximum salinity or average total concentration, being one of the primary factors determining zonation in salt marshes at these particular levels.

The highest tide in 1939 was 7.7 feet; in 1940, it was 7.5 feet. The larger number of high tides do not come during the best portion of the growing season. Only when storm and high tides combine are all the marsh plants inundated. The height of the water table is due to a combination of a large number of causes. Salt water is supplied by the ocean; fresh water by streams and creeks, rainfall and irrigation seepage. The soil is poorly aerated as compared with other soils, but tests show that air is present and that bubbles of it arise when disturbed. The light is intense. Evaporation is considerable in this type of climate. As to biotic factors, the birds, which are abundant in all the areas, exert little influence. Over twenty species of mollusks and crustaceans aid in aerating the marshlands and mud flats. Plants compete with each other in any given locality.

Man has disturbed each area in some way, such as by building roads and railroads, draining, farming, grazing, constructing airports and docks, dredging, building salt works, and other types of construction.

GENERAL NOTES ON VEGETATION

The vegetation of the marshland may be considered as a highly specialized plant society, the components of which have more tolerance to salt than species in surrounding plant areas. The vegetation may be conveniently divided into three zones: (1) lower littoral, (2) middle littoral, and (3) upper littoral. In the lower littoral are the algae, but the conspicuous flowering plant is Spartina, which grows in widely spread pure stands. Here there is exposure of the upper parts of the Spartina plants at low tides, and the almost complete to complete submergence at high tides where the plants grow in deeper water. The plants of the lower littoral are Batis, Salicornia, Spartina, Triglochin, Cladophora, Entermorpha, Ulva, Lyngbya, Rhizoclonium, and Ruppia.

In the middle littoral the principal plant is Salicornia which is usually associated with two or more genera as Distichlis, Suaeda, and others. This area lies between the lower area in which plants are bathed in tide water twice daily and that area in which plants are partially covered with salt water only with high tides. The genera present are Atriplex, Cordylanthus, Cotula, Cuscuta, Distichlis, Cyperus, Eleocharis, Ranunculus, Salicornia, Scirpus, and Suaeda.

The plants of the upper littoral are covered only by storm tides, while the ground is covered with water from only tho very high tides. The principal genera in this area are Atriplex, Distichlis, Frankenia, Limonium, Monanthochloe, and Suaeda. These species, except Limonium, are found generally distributed at all twelve stations, usually two or three associated, although pure stands may occur. The genera present in the upper littoral are Amblyopappus, Anemopsis, Aphanisma, Atriplex, Bromus, Capsella, Conyza, Cressa, Frankenia, Heliotropium, Jaumea, Juncus, Lasthenia, Lepturus, Limonium, Lotus, Monanthochloe, Pholiurus, Plantago, Pluchea, Sesuvium, Sonchus, Spergularia, and Suaeda.

There are about sixty species present. No trees are found in the marshlands, small willows and cottonwoods grow along creeks where there is hardly a trace of salt, and inland from storm tides. There are a few suffrutescent shrubs. Most of the plants are herbs, annuals, or perennials, growing on the marsh mud flats; a few species of algae and one seed plant, Ruppia, are present floating in the water. Table 2 gives a list of the species found below the storm tide level. There are some five or six species which one could hardly class as salt marsh plants, but as they are present at most stations and mingle with the salt marsh plants and exist even when covered by occasional dousing of salt water, they are included.

There are about nine really abundant plant genera commonly present throughout the twelve stations. These are *Atriplex* spp., Batis, Distichlis, Frankenia, Limonium, Monanthochloe, *Salicornia* spp., Spartina, and *Suaeda* spp.

Algae play an insignificant role in these marshlands. During any portion of the year but mostly in the early summer, mats of floating algae, principally Enteromorpha, are present in most of the bays and shallow water. With the advent of late summer, they are deposited on the bare ground as the water level decreases. Kelps and other marine plants are washed

TABLE 2. List of marsh species within storm tide limits with relative abundance.

Key: Va—very abundant
F—frequent
I—Infrequent

*Species**	
Amblyopappus pursillus H. & A.	I
Anemopsis californica Hook	I
Aphanisma blitoides Nutt	I
Atriplex hastata (L.) Gray	I
A. watsonii Nels	Va
A. semibaccata Brown	F
Batis maritima L.	Va
Bromus rigidus Roth	I
Capsella procumbens (L.) Fries. var. *Davidsonii* Munz	I
Cladophora sp.	I
Conyza coulteri Gray	I
Cordylanthus maritimus Nutt	F
Cotula coronopifolia L.	I
Cressa truxillensis H. B. K.	F
Cuscuta salina Engelm	F
C. salina Engelm. var. *squamigera* (Engelm.) Yuncker	F
Cyperus laevigatus L.	F
Distichlis spicata (Torr.) Rydb. var. *laxa* (Vasey) Fawcett and West	Va
Eleocharis mamillata Lindb. fil.	F
Enteromorpha crinita (Roth.) J. Ag.	F
E. intestinalis (L.) Link	I
E. flexuosa (Wulf.) J. Ag.	I
E. salina var.	F
E. tubulosa Kütz	I
Frankenia grandifolia C. & S.	Va
Heliotropium curassavicum L. var. *oculatum* (Heller) Jtn.	F
Jaumea carnosa (Less.) Gray	F
Juncus acutus L. var. *sphaerocarpus* Engelm	I
Lasthenia glabrata Lindl. var. *coulteri* Gray	I
Lepturus cylindricus (Willd.) Trin	I
Limonium mexicanum Blake	Va
Lotus strigosus (Nutt.) Greene	I
Lyngbya aestuarii f. ferruginea Gomont	I
Marsilea vestita Hook. & Grev	I
Monanthochloe littoralis Engelm	Va
Pholiurus incurvus (L.) Schinz & Thell	I
Plantago heterophylla Nutt	I
Pluchea camphorata (L.) DC	F
Ranunculus cymbalaria Pursh. var. *saximontanus* Fernald	I
Rhizoclonium tortuosum (Dillw.) Kütz	I
Ruppia maritima L.	I
Salicornia bigelovii Torr	F
S. depressa Standl	F
S. pacifica Standl	Va
S. subterminalis Parish	Va
Scirpus acutus Muhl	I
S. americanus Pers	I
S. californicus (Meyer) Britt	F
S. paludosus A. Nels	I
Sesuvium verrucosum Raf	I
S. sessile Pers	I
Sonchus asper L.	I
Spartina leiantha Benth	Va
Spergularia macrotheca (Hornem) Heynh	F
S. salina J. & C. Presl	F
Suaeda californica Wats	Va
S. californica Wats. var. *pubescens* Jeps	F
S. fruticosa Forsk	F
S. minuitiflora Wats	F
S. torreyana Wats	F
Triglochin maritima L.	F
Ulva latissima L.	F

* Identification of algae by Dr. G. J. Hollenberg, La Verne College, Calif. Nomenclature of other species according to Munz's *Southern California Botany* (1935).

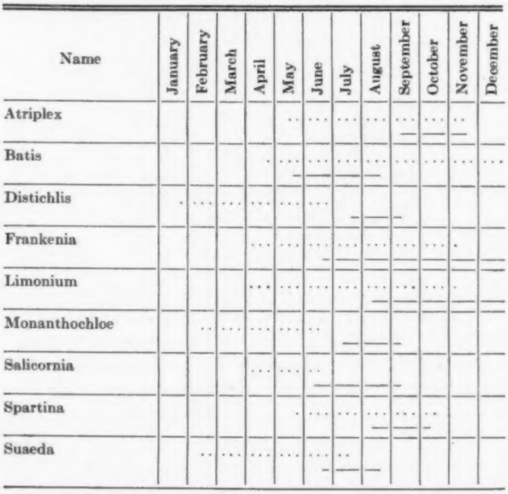
in with the tides but play no part in the marsh except to raise the ground level. This is in contrast to studies of conditions along the eastern coast, where a larger number of algae plants are present.

There is a gradation from salt marsh plants to those which are less salt tolerant. In some cases introduced plants, as some of our aggressive weeds, come in, but in most cases there is a tendency in two directions. In one, the vegetation changes from marsh plants to those sand dune plants which are found along the shore bordering the marshes, particularly where sand has blown into the marsh. This vegetation later yields to the chaparral. In the other case, marsh plants give place directly to the chaparral, which is the climax for this region.

As there is no frost, growth of the perennials is nearly continuous throughout the year, but with a decided slowing and almost cessation during the winter. The majority of the plants have their best growth during the late spring and in the summer months. As the winter season approaches, there is a slowing down of growth and death of the annuals. There is a lag in the growing season of the marsh plants as compared with those on land.

In Figure 7 is given the time of flowering and of

FIG. 7. Periods of growth and flowering for the principal genera during 1940.*



*Dotted line represents period of vigorous growth; straight line, flowering.

growth of the principal genera during a year's period. The other genera also follow this general trend. As the year advances, plants on flat areas where there is poor drainage begin to look sickly, although those along the edges of ditches and other channels are still luxuriant. In late autumn the marshes are beautiful with the red coloring from the anthocyanin in the succulent leaves of Suaeda and the stems of Salicornia. Acres of Spartina in Mission Bay (station 3) look like rich fields of grain. Flowering extends over all the season but is most abundant during the summer and autumn. At this time tides are low and plants are not likely to be submerged.

The composition of the salt marsh is such that few individual plants can be distinguished in the mass of vegetation, the exception being individual plants of Limonium with their large, leathery leaves and the lavender-tinted flower clusters. Inasmuch as most of the marsh plants grow over each other, as Frankenia or the grasses, or under each other with their rhizome propagation as Spartina, it is next to impossible to get a true representation of the density of a stand in relation to the individual plants. In the quadrat studies, therefore, all the shoots coming from the ground were counted, although they may have represented only one original plant with its ramifications of stems (partially buried) or rhizomes. Few pure stands were found, Salicornia and Spartina being the principal exceptions. In counting, a square meter, divided into 100 decimeters, was used. Each number represents the count in one square meter. Additional counts may be found under the study of the individual plants. The relative density of the nine principal genera is given as follows: (1) Spartina 425 aerial stems per square meter; (2) Salicornia 3,700 young plants; (3) Batis 74 aerial shoots; (4) Distichlis 810 aerial stems; (5) Monanthochloe 3,600 aerial stems; (6) Suaeda 8 plants, Frankenia 45 (no pure stands of Suaeda were found); (7) Limonium 4 plants, Salicornia (young plants) 2,700; (8) Frankenia 660 aerial stems; Distichlis 70 aerial stems; (9) Atriplex 2 plants, Distichlis 15 aerial stems.

In December, 1939, mud flats were covered with seedlings of Salicornia species. Counts were made in square decimeters with the following results: 136, 143, 174, 175, 185, 187, 192, and 216, respectively.

Zonation is seen at all stations but particularly in the slight rise of ground at the upper edges of some of the locations. The transition from one community to the one directly above it is possible when the rise of the ground may be but one inch in a foot. In the deeper water is the Spartina community, occasionally Spartina and Salicornia; higher, rather infrequently pure stands of Salicornia, Salicornia and Distichlis or Salicornia and Suaeda; a little higher, combinations of any of these plants—Salicornia, Distichlis, Frankenia, Suaeda, Limonium, Monanthochloe; and again on still higher ground, combinations of Distichlis, Frankenia, Limonium, Monanthochloe, Atriplex, Cordylanthus, Jaumea, Heliotropium, and Spergularia.

Where fresh water seeps into the area, the zonation is different in that Scirpus species are found along with some of the salt marsh species which grow in less saline places. This transition from fresh to brackish water is interesting. There is no clear line of demarcation between fresh- and salt-water species; it varies from year to year in the areas. It is influenced by the tides and precipitation as well as by irrigation seepage.

While Spartina tolerates the largest amount of covering by the water, Salicornia stands a greater

diversity than any other plant although Distichlis and Frankenia are close seconds. The two latter grow well when occasionally submerged and can be found in areas where the salt content is low. Chapman (1939) states that the primary factor determining zonation is not the maximum chloride concentration but rather the average total chloride concentration throughout the year may be more important.

Tests show that there is an increased salinity as depth in the soil increases. The roots are, therefore, in direct contact with soils containing varied percentages of salts. All plants are shallow rooted compared with those of the sand dune and chaparral communities nearby. Those which are the most shallow rooted do not have their roots in contact with as much salinity as those which are more deeply rooted. The depths at which the principal plants are rooted is given under the individual study of each.

SUCCESSION

Succession is from hydric to mesic. Spartina, the pioneer, is the most tolerant to water. Then, after it has been growing in a given spot and the dead parts of Spartina have accumulated and perhaps debris has been left by storms, Salicornia gains a foothold, often growing with Spartina. Then as the area has less and less water standing on it continually, Salicornia is found in pure stands. Salicornia characterizes the second stage. It needs some aeration in the soil. It does not do well even above water level if the soil is excessively compact, with little air, just as it does not do well in standing water where there is little aeration. It does not survive where it is totally submerged. All the species of Salicornia seem to have about the same requirements as regards aeration. The next stage is that in which plants are usually partly submerged daily, as Batis, Monanthochloe, Distichlis, and Suaeda. Limonium is associated with all of the above except Batis, as Batis maintains itself on slightly lower flats. Then on higher ground there are various species of Atriplex, associated with Frankenia and above, out of the reach of the storm waves, Aplopappus and other genera which are not saline.

ECONOMIC IMPORTANCE

The importance of low, flat areas between coastal bluffs, especially in the vicinity of cities, is easily recognized. With drainage or fill, these areas become of value for business and residential sites as in the case around San Diego and Mission bays. Where land is not so valuable, but where its flatness is appreciated, airplane fields and race tracks have been laid out.

In some of the marshes, particularly that of San Diego Bay, salt works are of importance. Several areas are important as bird sanctuaries. Species of birds, almost extinct, are increasing in number. Clams are obtained from several mud flat areas. Fishing, boating and swimming are enjoyed. Where areas are not bird sanctuaries, hunting is permitted. Ranches and pasture lands are found where the salinity of the soil is low.

INDIVIDUAL STUDIES OF PRINCIPAL SPECIES

There are about sixty species found in the marshlands of this county. Of these nine were chosen as the principal species for study because of their abundance in varying localities. These are species of Spartina, Salicornia, Batis, Distichlis, Monanthochloe, Suaeda, Limonium, Frankenia, and Atriplex.

Spartina leiantha Benth.

This is the tallest and coarsest of the nine principal species of the salt marshes. It is found farthest in the water, partly submerged, where it is flooded twice a day and frequently completely submerged with the high tides. Only during low tides can one walk out into the clumps nearest shore and then with considerable insecurity of footing. As it is farthest out in the water, it offers the first barrier to the storms and gives protection to the association landward.

Spartina, growing in deeper water than any other genus, has its best development when it is partially submerged. Its best growth in the entire area is at Mission Bay (station 3), where the temperature of the water and soil and the salinity are fairly uniform as compared with other stations. It is found in full sunlight, receiving the direct sun except where neighboring plants of like kind shade it. It grows principally on low mud flats, but it is also found in areas where the wind has blown sand into the bays or sloughs. During the summer there is a gradual increase in salinity in the water in which Spartina grows, as shown in Figure 5. Where a small amount of fresh water has seeped in, it is doing poorly.

Success in the horizontal distribution of Spartina is due to its ability to stand submergence frequently. Migration into lower areas is prevented by the depth of the water covering it. Its distribution upwards into shallower water is prevented by Salicornia and other genera. Checks at the same time show the following: salinity in parts per thousand at San Diego Bay, Spartina association 38.40, Salicornia association 39.20; at Soledad station, Spartina association 37.01, Salicornia 38.61; and at Buena Vista station, Spartina 21.76 and Salicornia 22.48. While this is not a great difference in salinity, it may be that this difference is sufficient, along with the factor of aeration, to condition the distribution of these two plants —Spartina in deeper water, Salicornia in shallower water with greater salinity.

Because of its rhizome habit, Spartina is able to spread from a common center, branching freely and forming huge mats which are not disturbed by tide or current, and often cover several acres. Its coarse, leathery leaves permit the passage of water without much breaking, except in severe storms which bring debris and break the aerial stems or leave refuse covering them.

With its horizontal rhizomes on an average of 13.5 cm. below the surface, from which arise at each node aerial stems, Spartina forms an almost impenetrable turf into which it is difficult to cut. It is impossible, therefore, to select a single plant, for even at the outer edges of the clumps it is closely woven together. Counts showed 425, 432, and 480 aerial stems per square meter. Figure 8A gives the vertical appearance of the plant, with figure 8B the horizontal layout of the root system.

The rhizomes are about 0.39 cm. in diameter, and the actively growing tips are about 2 to 3 decimeters long. The rhizome consists of many short internodes, less than 1 decimeter long, interrupted by numerous nodes, at which arise upright shoots. The terminal bud at the end of each horizontal main axis remains horizontal, but the lateral shoots turn upward and develop into aerial shoots.

At flowering time the aerial shoots reach an average height of 93.2 cm. They flower profusely, no matter how densely crowded. The aerial shoots average 480 plants per square meter. The diameter of the aerial stem is 0.62 centimeters at the base. Internodes average 4.12 cm. in length. About eight green leaves appear at a time, averaging 30.2 cm. in length and 0.73 cm. in width. The wind-pollinated flowers appear in August and set seed in October. Seedlings are uncommon, the plant spreading vegetatively.

The root system is fibrous, made up of relatively short, tough roots, intertwining in the soil and making a dense turf.

The leaf of Spartina shows the rolled type of leaf typical of the grasses, with deep sinuses running half way in from the dorsal side. The dorsal surface is covered by a rather thick layer of cuticle which extends out in conelike projections, in length about one-half the diameter of the epidermis. The protruding cuticle frequently overlaps in the sinuses. The stomata, confined to the sinuses, have cuticle partially covering the stomatal pore. Each stoma has two subsidiary cells. Several rows of sclerenchyma stiffen the protruding portion of the leaf. Several rows of small chlorenchyma cells are present, extending almost to the lower surface. In this area next to the epidermis are specialized cells at times connecting with the outside. Water-storing cells fill the ridge below the sclerenchyma until the fibrovascular bundle is reached. There are usually some sclerenchyma cells around the bundle. Between the vascular bundle and the lower epidermis is a patch of sclerenchyma. A large air space, located below the sinus, separates each bundle. No crystals are present. The lower epidermis is small, heavy-walled, even, compact, and covered with cuticle in thickness nearly one-half the diameter of the epidermal cells. There is a large amount of phloem and xylem. (Fig. 8C).

The stem is a monocotyledonous type with vascular bundles scattered throughout the pith. The epidermis is thin, with walls about equal in thickness, and with a thin layer of cuticle. There are few stomata. Thickened walls of the cortical parenchyma appear on the cells for three layers below the epidermis. All are compactly placed. Next are six rows of larger, thin-walled cortical parenchyma cells, while to the inside is a band of small, thin-walled parenchyma cells, with dense cytoplasm and conspicuous nuclei. This layer, with more intercellular spaces than the outside, has its cells break down forming lacunas. At the inner side of these cells there is a layer of sclerenchyma about five cells in thickness, inside of which is the pith parenchyma with few vascular bundles. No crystals or tannin are present (Fig. 8D).

The epidermal cells of the rhizome are small and compact. No cuticle appears to cover them. Inside are about three rows of large, thin-walled cells with no intercellular spaces. Huge lacunas, filling one half of the tissue of the rhizome, are placed regularly, intercepted by two-celled rows of parenchyma. To the inside, the parenchyma, composed of large cells, is traversed by scattered vascular bundles, surrounding a single huge lacuna (Fig. 8E).

The root is composed principally of cortical parenchyma. The epidermis, composed of small cells, has four to five rows of sclerenchyma inside of it. No cork is developed. Then, inside, the cells of the cortical parenchyma are larger, breaking down into lacunas, which are separated by one or more rows of cells. The endodermis consists of cubical, thick-walled cells, while the pericycle is inconspicuous. The steele is made up of a few tracheae surrounded by sclerenchyma. The phloem is inconspicuous (Fig. 8F).

Spartina has the typical xerophytic rolled type of grass leaf, and with its thick cuticle and small protected stomata, lives in a physiologically dry habitat, although covered by salt water which it may not use. Air accumulation is conspicuous in the roots and rhizomes, which grow in poorly aerated mud, and also present, although less abundant, in the aerial stems and leaves. Johnson and York (1915) mention that there is a good system of air passage and air accumulation throughout the species of Spartina on the eastern seaboard. Its lower limit of vertical distribution is determined by the duration and depth of submergence; its horizontal distribution is influenced by its chief competitor, Salicornia.

Salicornia pacifica Stand.

Salicornia is found growing with Spartina in rather deep water or in pure stands in less wet areas. It is also present in mixed stands with Frankenia, Distichlis, and others. It does not invade the Spartina areas until sufficient debris is present to raise the level of the ground. Both annual and perennial species of Salicornia are present; and while they do not all have exactly the same requirements, the perennial, *Salicornia pacifica,* is distributed both in water and in drier situations, a slightly more extensive distribution than the annual species. It endures complete submerging, but not daily, and does not grow luxuriantly when mixed with Spartina, as Salicornia needs aeration and cannot be cut off from its gas supply for as long a time as Spartina. The effect of

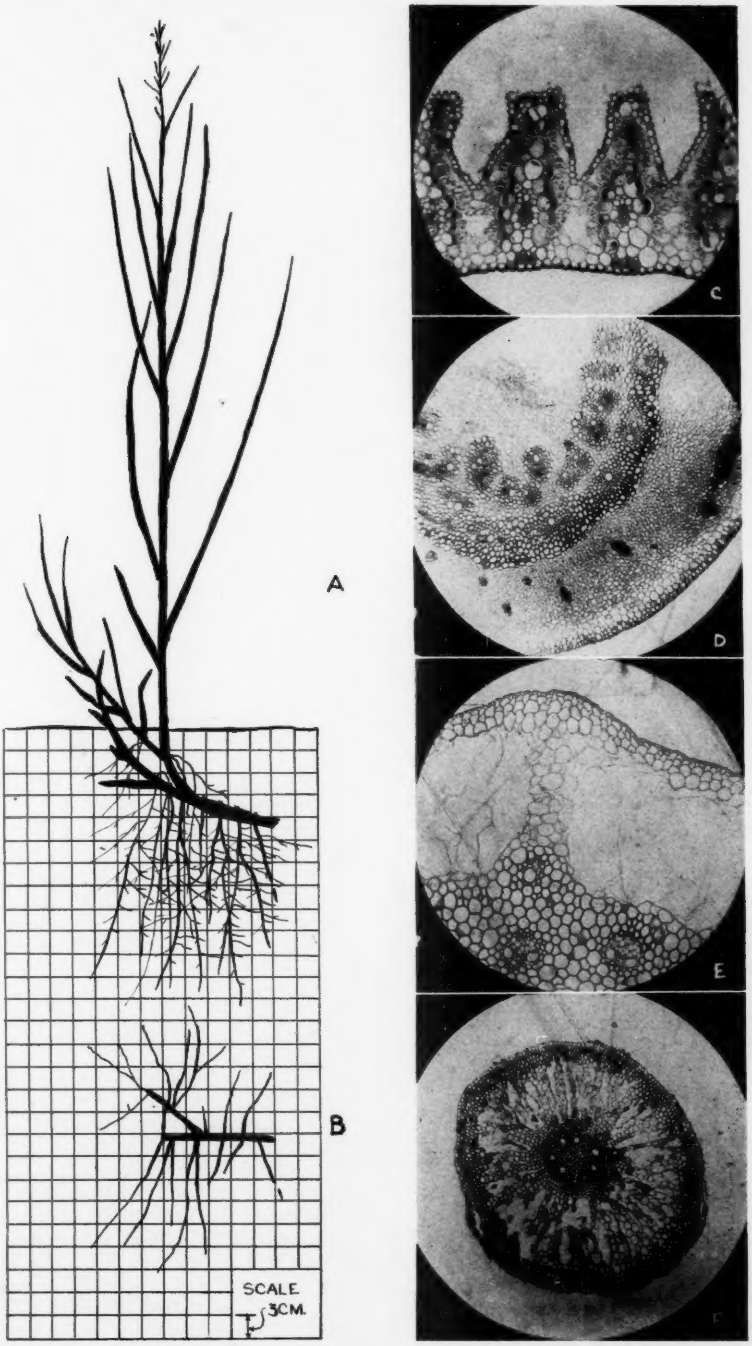


FIG. 8. *Spartina leiantha* Benth.

A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of blade.
D. Cross section of aerial stem.
E. Cross section of rhizome.
F. Cross section of root.

drainage and aeration is noticeable along the edges of ditches, as here it presents its most luxuriant stands; back from the ditches where the soil is low and compact, and conditions for growing are poor, it is weak and low-growing. Salicornia is present on ground which has a higher salt concentration than Spartina, for the soil water becomes more concentrated by evaporation and is less washed out by tides. As it grows luxuriantly only when aerated, even when salinity is considerable, it appears to be limited not so much by salinity as by the amount of aeration in the soil. It grows in full sunlight, particularly well in mud.

From October until spring, Salicornia gives a beautiful red coloring to the marshlands because of a development of anthocyanin in its stems. Cuscuta is a parasite on Salicornia.

The annual species of Salicornia appears most frequently invading bare areas, on flats where the drainage has been improved as well as in the places where it grew the preceding year. Seedlings appear most abundantly after the first heavy winter rains, as the salts washed out during the rains make less concentration at time of germination.

Salicornia pacifica is a suffrutescent perennial with a large number of stems at the base. It reaches an average height of 66.66 cm. and has joints up to 2.0 cm. long. Instead of becoming taller, the longer succulent branches become decumbent with their tips erect. The branching is opposite. It makes a dense growth in pure stands of an average of 3,700 aerial stems per square meter. It makes its best growth in spring and summer. Its minute flowers, sunken in the cavities of the internodes, appear in June. It is wind pollinated. Its roots are fibrous and not extensive (Fig. 9A and B).

The leaves are scalelike. The succulent stems are covered with a thick layer of cuticle under which the small-celled epidermis has a few small stomata which are slightly sunken. Inside is palisade tissue, several rows in thickness, intercepted by frequent groups of large water-storing cells. The inner cortical tissue is composed of large-celled, loosely-placed water-storing parenchyma in which are occasional leaf traces and an irregular row of sclerenchyma cells next to the endodermis which appear to develop into fiber cells. The endodermis is composed of a compact row of thin-walled cells. The central cylinder has secondary tissue made up of rows of phloem, cambium, and xylem enclosing pith, with the primary vascular bundles in the xylem near the pith (Fig. 9C).

The root is covered with epidermis which sloughs off leaving a layer of thin-walled phellem four or five cells in thickness. Inside, the cortical parenchyma contains stored starch, with large intercellular spaces. The central cylinder consists entirely of concentric rings of secondary phloem and xylem surrounding primary vascular tissue (Fig. 9D).

Salicornia is a typical halophyte with a high rate of transpiration per unit of surface area (Delf 1911). It has a reduced surface with succulent stems doing the work of the leaves. The limited amount of air which is stored in the intercellular spaces and in the air-storing tracheids appears to give it enough air to tide it over an occasional immersion. Its distribution is limited on its lower margin by depth and length of submergence, on its upper margin by competition with Frankenia, Distichlis, and Monanthochloe.

Batis maritima L.

Batis, which is of prostrate habit, is found growing on flat, low land, and develops rapidly by means of its horizontal stems from which arise short upright branches. In competition with other plants, it may grow upright and sometimes over them. Its growth is luxuriant during the late winter months. In many places the annual species of Salicornia dies, affording spread to the Batis plants. At high tides Batis bears complete submerging, but it usually grows on the bare, wet soil. The lengths of branches of three plants are as follows: one plant with four main branches, 140, 208, 210, and 281 cm. long; a second with five branches at 140, 205, 220, 282 and 360 cm; and a third with three branches 180, 230, and 255 cm. long. The plant averages 22.4 cm. above ground. In one square meter 74 aerial stems appeared from prostrate stems. The plant has dioecious flowers in sessile, crowded catkins. They are wind pollinated. Plants are woody at base and sometimes root at nodes along the older portions of the stems. A fibrous root system develops at each node and extends to an average depth of 17.0 cm (Fig. 10A and B).

Batis is a malacophyllus plant possessed of opposite, linear-oblanceolate, succulent leaves on an average of 2.24 cm. long and 0.46 cm. wide. They are flat on the dorsal side and convex on the ventral. The cuticle is rather thick, covering the large epidermal cells which have no trichomes. A few slightly sunken stomata, almost covered with cuticle, are present on both surfaces. Solereder (1908) states: "An important feature in the structure of the leaf lies in the fact that the stoma is enclosed by two semilunar subsidiary cells arranged parallel to the transverse with regard to the longitudinal axis of the narrow leaf." Inside the epidermis is a layer of chlorenchyma about four cells in thickness made up of cells which are so nearly cubicle that they can hardly be called palisade. In this layer, principally on the ventral surface, are a very few small calcium oxalate druses. Just inside this layer is a number of small vascular bundles, the xylem being placed in each bundle toward the center of the leaf. Nine tenths of the rest of the leaf is water-storage tissue made up of large parenchyma cells with one vascular bundle in the center of the leaf (Fig. 10C).

The stem is not as succulent as the leaf. It is overlaid with a heavy layer of cuticle, about one-sixth the diameter of the small, compact, epidermal cells. The stomata are few and sunken. There are no trichomes. Below the epidermis is a compact row of cells, the phelloderm, to the inside, of which are

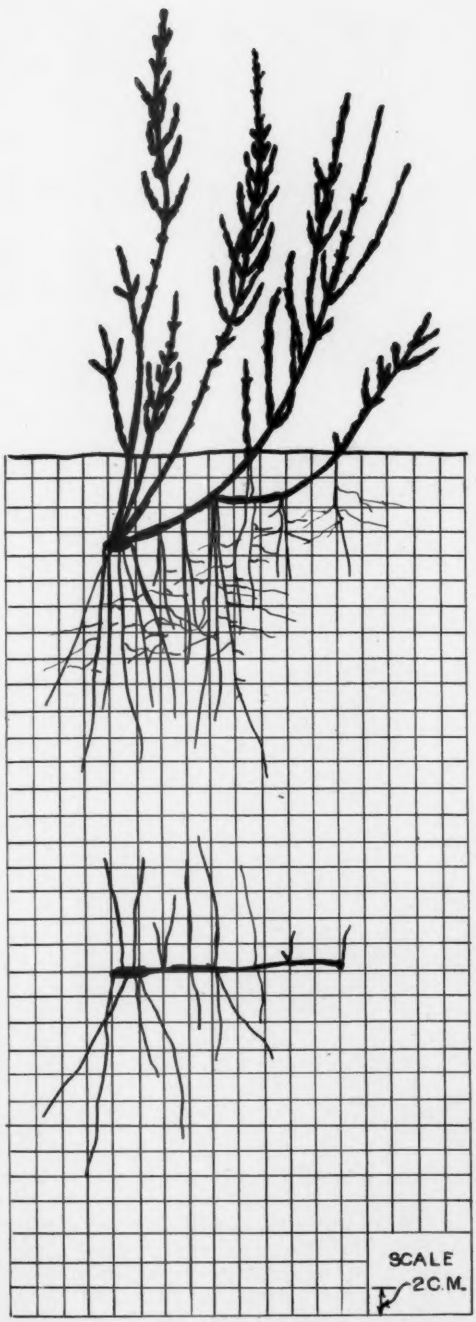
about six rows of spherical chlorenchyma cells intercepted by cells without chloroplasts and by small intercellular spaces. These cells give way to parenchyma cells. The central cylinder is composed of vascular bundles with pith parenchyma in the center. Fiber cells are present in the vascular bundles. Calcium oxalate is present as druses (Fig. 10D).

The root is covered by several rows of cork cells, the outer layer having dropped off. Inside is a single row of cortical parenchyma separating lacunas. Phloem, cambium, and xylem fill the central cylinder which surrounds the protoxylem. There are a few protoxylem cells extending into the older metaxylem cells.

In summary, Batis is a prostrate succulent with fleshy leaves and stems, growing on mud flats where it is subjected to immersion by tides. It is abundantly supplied not only with water-storage cells but with small intercellular spaces and numerous lacunas, the latter principally in the roots. It is thus adapted to having its roots in poorly aerated saline soil, while its upper parts have sufficient air to tide it over occasional periods of submergence.

Distichlis spicata (Torr.) Rydb. var. *laxa* (Vasey) Fawcett & West

This perennial plant of the upper littoral is associated with Salicornia, Monanthochloe, Suaeda, Atri-



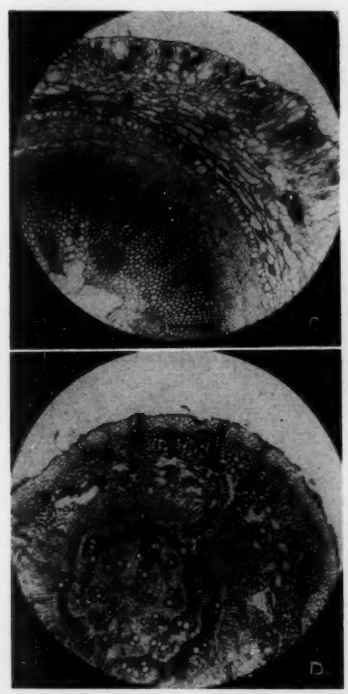


FIG. 9. *Salicornia pacifica* Standl.
A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of stem.
D. Cross section of root.

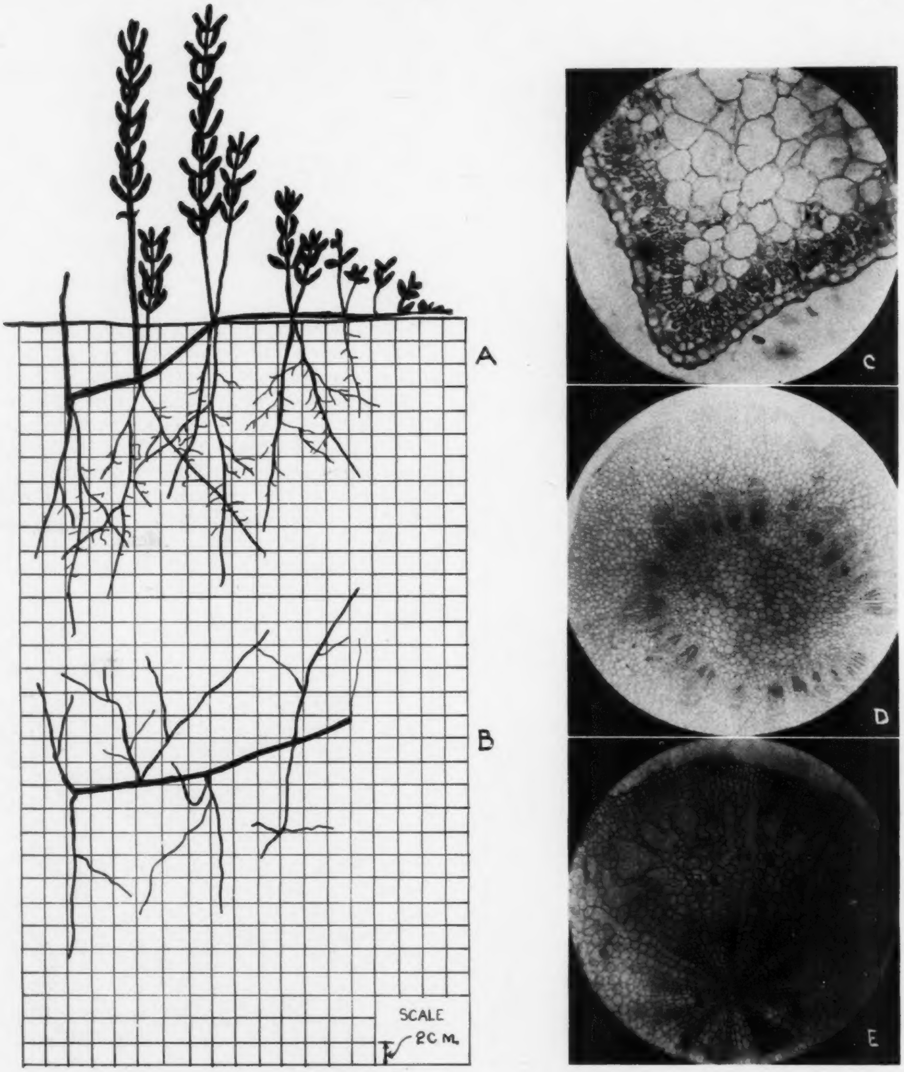


FIG. 10. *Batis maritima* L.

A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of leaf.
D. Cross section of stem.
E. Cross section of root.

plex, and Frankenia. Its salt tolerance is varied, ranging from situations where it is flooded daily to where it is covered by salt water only periodically during storm tides. It is almost as versatile as Salicornia, for it grows where the soil is wet and where it is daily submerged to a position on the top of ridges of 2 to 2½ meter sand dunes encroaching on the marshland. It starts its growth at lower levels, and as it is covered by sand, it grows upward. It grows equally well in sand or silt, with the best growth above the high tide but not beyond the reaches of the storm tides. It is not found in fresh-water areas. It does not extend far into lower levels, as it meets too much competition with Salicornia which requires less air, while above it meets competition with a great variety of plants which succeed under less salinity and require better aeration.

Distichlis spreads principally by means of rhizomes. When growing where there is plenty of room, it has scaly rhizomes on an average of 8.0 cm. below the surface. But at times when it is crowded, it develops horizontal aerial stems with upright tips

which spread out over the surrounding vegetation. The plants stand full sunlight.

The aerial stems with their leaves measure 21.8 cm. in height. An average of 810 aerial stems was found in a square meter. In one square meter there were 41 aerial stems of Distichlis, 148 plants of Triglochin and 492 young plants of Salicornia. In another square meter, there were 54 Distichlis and 7 Limonium plants. Distichlis is not found in pure stands. The length of the blade is 4.5 cm., the width when unrolled 0.28 cm. Because of its extensive rhizome system an individual plant may spread over a number of square meters. The root system is fibrous, numerous roots appearing at each of the nodes of the rhizome (Fig. 11A and B).

The partially rolled leaf is made up of sections of vascular bundles, surrounded by food-storage cells and chlorenchyma, each section being separated by water cells. The upper epidermis is furrowed, having a sinus at each portion of water tissue. The cells of the upper epidermis are irregular in size and shape, and are covered by a heavy layer of cuticle. The thickness of this cuticle is about one-sixth the diameter of an average-sized cell, and extends out in conelike projections. Stomata with their subsidiary cells appear along the sides of the sinuses. The cuticle partially closes the stomatal pore.

Directly below the upper epidermis there is a cluster of sclerenchymatous cells with a band of small-celled chlorenchyma two cells in thickness, on either side reaching to the lower epidermis. To the inside is a band of huge food-storage cells. In the center is one vascular bundle surrounded by a row of sclerenchyma. At the lower portion of each vascular bundle is another cluster of sclerenchyma similar to that on the upper surface.

Two rows of water-storage cells separate each section of the leaf with its vascular bundle and its surrounding food-storage cells and chlorenchyma. There is little intercellular air space and few air-storage cells.

The irregular-shaped cells of the lower epidermis vary in size, some being about three times the diameter of others. The stomatal pore is partially covered by cuticle. The cuticle is similar in appearance with that of the upper epidermis (Fig. 11C).

Next to the lower epidermis of the leaf sheath are several rows of sclerenchymatous cells, while the center is made up of large lacunas, separated by vascular bundles and a few parenchyma cells.

The aerial stem is very tough and wiry. The epidermis is small, compact and encloses about five or six rows of sclerenchymatous tissue, the outer half being fibrous in character. To the inside are large lacunas separated by irregular-shaped parenchyma cells. A row of compact, spherical, parenchyma-like cells appear to the inside. The endodermis is very thick-walled to the inside. The stele is filled with scattered vascular bundles separated by fiber cells and parenchymatous cells filled with starch grains (Fig. 11D).

Within the small-celled epidermis of the rhizome is a band of approximately five rows of slightly lignified cells, and inside thinner-walled cells irregular in shape, with many large intercellular spaces. The endodermis is fairly regular. The stele consists of a band of sclerenchymatous tissue inside of which are numerous vascular bundles with large tracheae intercepted with small-celled parenchyma, the latter being predominant in the center. There are few intercellular spaces (Fig. 11E).

Below the regular-shaped cells of the epidermis of the root are three rows of cells showing slight lignification. The rest of the cortex is composed of huge air spaces and to the inside a band of six rows of small cortical cells with intercellular spaces. The endodermis and pericycle are regular in shape. The rest of the stele is made up mostly of sclerenchymatous tissue with a number of large tracheae, some smaller ones and a few phloem cells (Fig. 11F).

Distichlis is an aggressive member of the marsh plant association because of its means of spreading by rhizomes. It is adaptable, too, to rise when covered, either by means of raising its new rhizomes in the soil or by means of spreading its aerial stems over other plants. Its rolled type of leaf makes it possible to reduce its water loss. The leaf blade is very compact with small air-storage space, but the leaf sheath as well as the aerial stem have large-sized lacunas. The root has abundant intercellular spaces. Distichlis can, therefore, withstand occasional submergence. Johnson and York (1915) state that its absence from wet areas may mean that it meets other competitors or meets some of its usual competitors at a greater disadvantage on wet soils. From the study of its anatomy (as given above) it would seem that its ability to compete is due to its xeric character and its effective air accumulation for a limited time.

Monanthochloe littoralis Engelm.

This perennial grows in great colonies and spreads principally by means of its wiry stems. The location of Monanthochloe in the upper littoral indicates that it can stand coverage by high tides or storm tides. It stands full sunlight. In one square meter 39 aerial stems of Monanthochloe, 2 Salicornia and 1 Frankenia plants were counted. In pure stands, counts per square meter showed 2,800, 3,100, 3,600 and 4,400 aerial stems, respectively. The aerial branches are short and unless growing densely soon become decumbent. They grow on an average of 23.5 cm. above the surface of the soil. The internodes average 5.7 cm. The leaves are minute, in clusters at the ends of the short branches. The leaf blades are 5.9 mm. long and 1.4 mm. wide when unrolled. The plant is dioecious, with three to five flowered spikelets, which are quite inconspicuous (Fig. 12A).

The rhizome, on an average of 1.8 cm. below the surface, is stout, with short internodes. The fibrous roots are crowded, numerous and thin (Fig. 12B).

The partially rolled leaf is made up of triangular sections of tissues surrounding a vascular bundle each of which is separated by water-storage cells. The

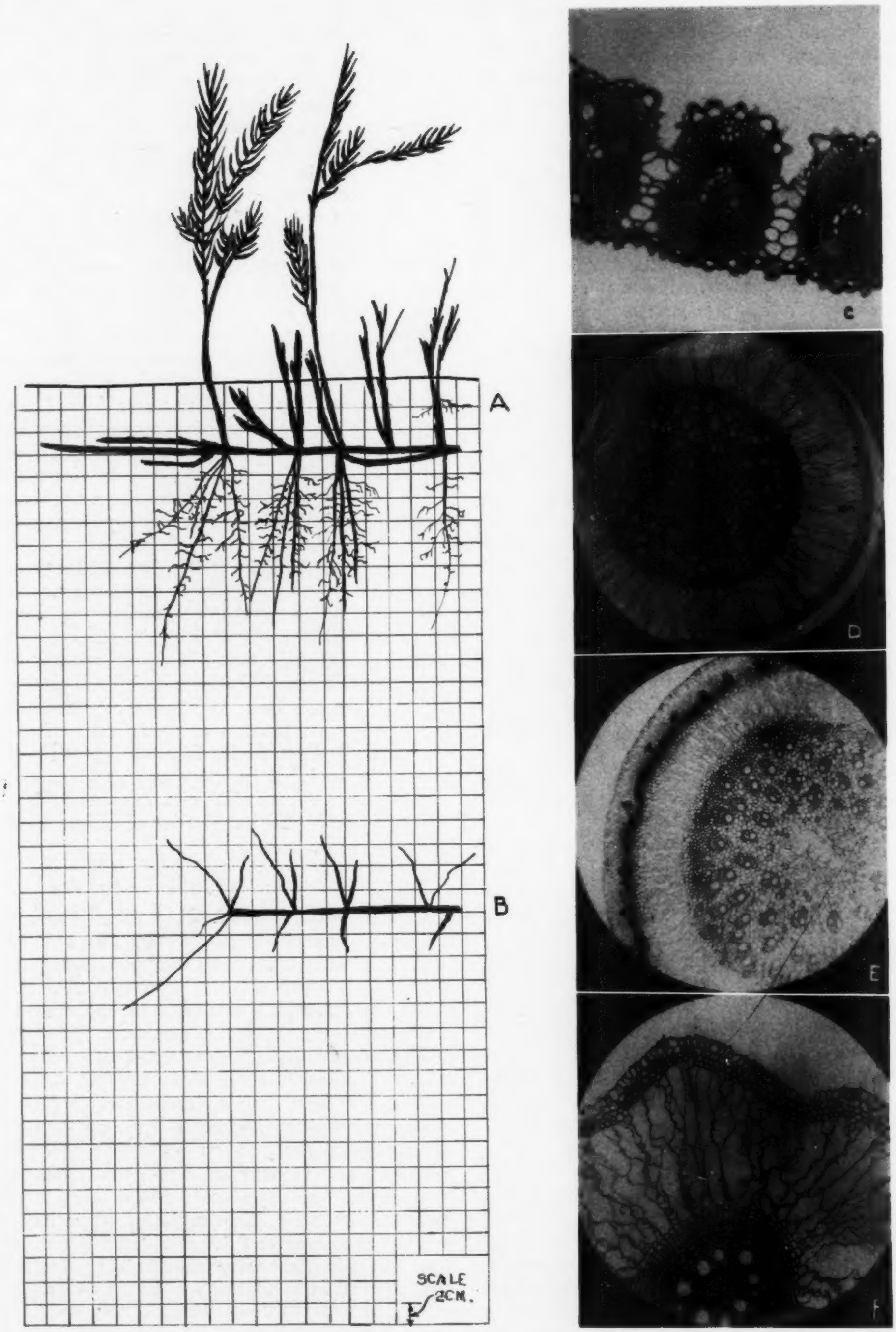


FIG. 11. *Distichlis spicata (Torr.) Rydb. var. laxa (Vasey) Fawcett & West.*

A. Vertical section of plant.
B. Horizontal section of root system.
C. Cross section of leaf.
D. Cross section of aerial stem.
E. Cross section of rhizome.
F. Cross section of root.

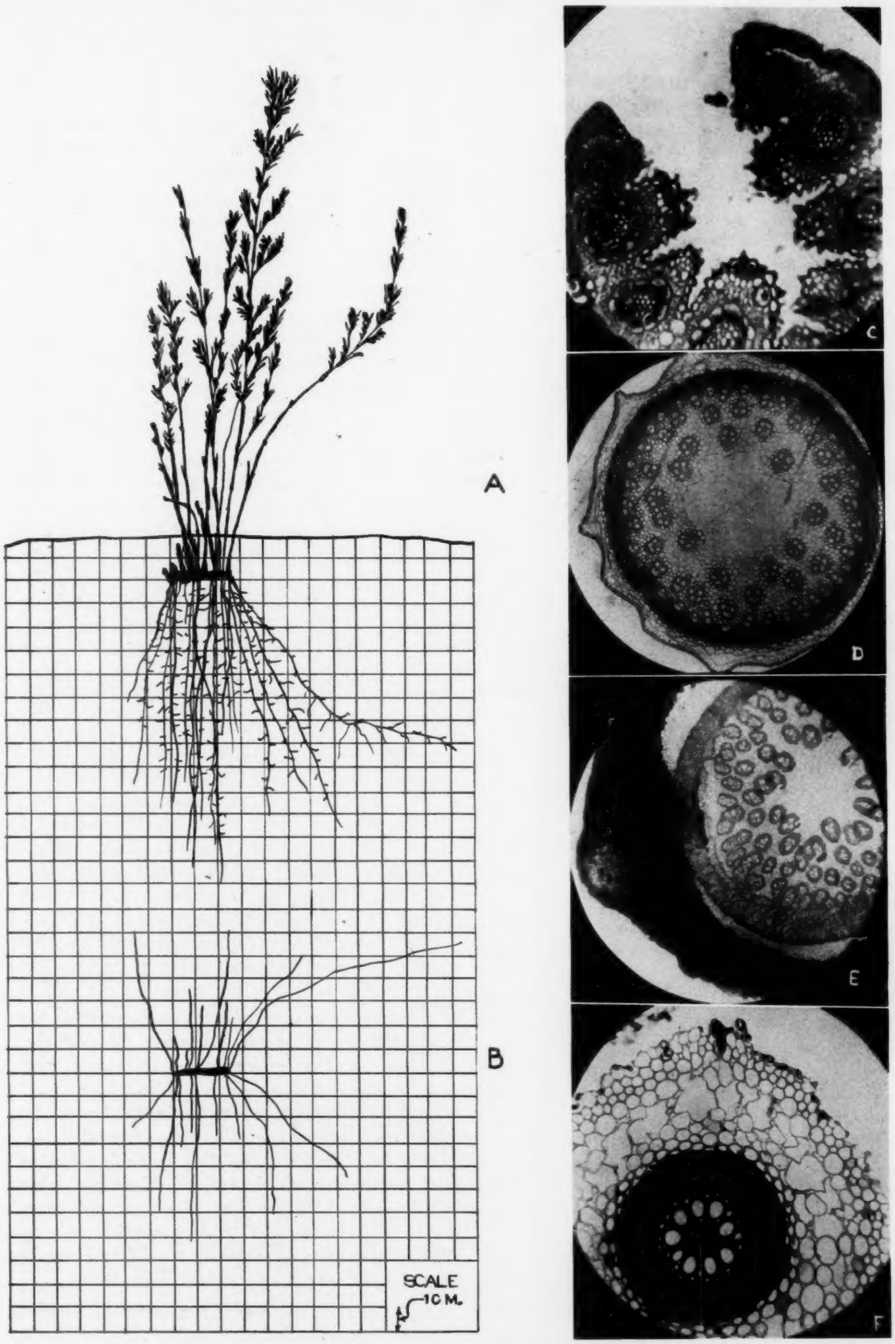


FIG. 12. *Monanthochloe littoralis* Engelm.

A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of leaf.
D. Cross section of aerial stem.
E. Cross section of rhizome.
F. Cross section of root.

upper epidermal surface consists of heavy-walled, irregular-shaped and sized cells, covered by a heavy layer of cuticle, with conical projections of the cuticle extending outward. In the sinuses these projections overlap slightly. Stomata are found in the sinuses.

At the tip, just inside of the upper epidermis is found a small group of fiber cells about three to four cells in thickness. Inside are two to three rows of chlorenchyma, in which are occasional large specialized cells. The chlorenchyma completely surrounds the vascular bundle, which in turn is overlaid by a single row of large-sized food-storage cells. The mesophyll is compact. Below is a patch of sclerenchyma about four cells in thickness adjoining the lower epidermis, which is composed of very heavy-walled, regular cells except at the sinuses, where the cells are larger. A group of specialized cells is usually found in the epidermis at the point where the water cells of the sinus touch the epidermis. No stomata are found in the lower epidermis which is covered by a thick layer of cuticle (Fig. 12C).

The aerial stem is covered by an epidermis of heavy-walled extremely small cells, inside of which are two rows of small-celled sclerenchyma. The cortical cells inside are about ten rows in thickness with intercellular spaces throughout. To the inside are about six rows of small sclerenchyma cells with another six rows of fiber cells. The remainder of the stele is composed of parenchyma, in which are scattered vascular bundles with a large air space in the center (Fig. 12D).

The rhizome is thick as compared with the aerial stem. Inside the epidermis the cortical layer consists of a band of lignified cells with rows of fiber cells and to the inside a band of small parenchyma cells. The stele has a wide band of fiber cells which surround parenchyma cells, in which are many scattered vascular bundles (Fig. 12E).

The roots are all very small. Inside the epidermis the parenchyma is partially broken down into intercellular spaces, while next to the stele it is lignified. The endodermis also is lignified. The stele is made up of sclerenchymatous tissue with the vascular bundles contain'ng large tracheae (Fig. 12F).

Monanthochloe has intercellular spaces in its roots, rhizomes and stems, although its leaves are very compact. This permits its growth in soil which is lacking in aeration from time to time, but the leaves do not stand much submergence. Its distribution is limited primarily by submergence on its lower limits and competition with associated species on its upper limits.

Suaeda californica Wats.

Suaeda is found mostly in the upper littoral belt, where it is seldom completely submerged. It grows both in sandy and clayey soils but appears to grow best in sand or on areas covered by tidal trash which are slightly ra'sed above the surrounding areas and where the aeration is improved. It has not been found in or near fresh water. Its roots can grow in wet, saline soils.

Suaeda does not grow in pure stands, being usually associated with Salicornia, Distichlis, Monanthochloe, and Frankenia. It does not appear to be so aggressive as its associates. Individual plants may shadow their neighbors, but as they do not have vegetative means of reproduction, such as rhizomes or runners, their entrance into unoccupied areas, such as places usually built up by tidal trash, is by means of seeds. A large number of individual plants were found to cover an area larger than a square meter. Where the plants were smaller, some of the counts were as follows: Suaeda 8, Frankenia 45; Suaeda 9, Monanthochloe (aerial stems) 129; Suaeda 8, Distichlis (aerial stems) 214. Its best growth is in April and May; its poorest, in December. It stands full sunlight, but as the leaves overlap they afford some protection to those below them.

Suaeda is represented by five species, the most abundant being *Suaeda californica*. The suffrutescent perennial grows to an average height of 39.9 cm., branching widely, an average of 34.8 cm., ascending or decumbent. It is glabrous, with numerous crowded leaves. The leaves are succulent, flat on top, rounded below, and averaging 3.4 cm. long and 0.32 cm. wide. The flowers are small, greenish, perfect or unisexual, and wind pollinated. The fruit, a utricle, is wind disseminated. The stems, fleshy when young, become tough and woody at the base of the plant. Its roots are extensive, usually dividing at about 10.0 cm. below the surface (Fig. 13A and B).

The succulent leaf is covered with large, closely-placed thin-walled epidermal cells. The stomata are few. The layer of cuticle covering the epidermis is quite thick in fresh material. Inside the epidermis is a row or two of palisade. The rest of the leaf is filled with huge water-storage cells which contain a few chloroplasts in which are some soluble proteins. Occasionally anthocyanin is present. The vascular bundles, alternating with large parenchymatous cells, are abundant across the center of the leaf. No crystals or mucilage are present (Fig. 13C).

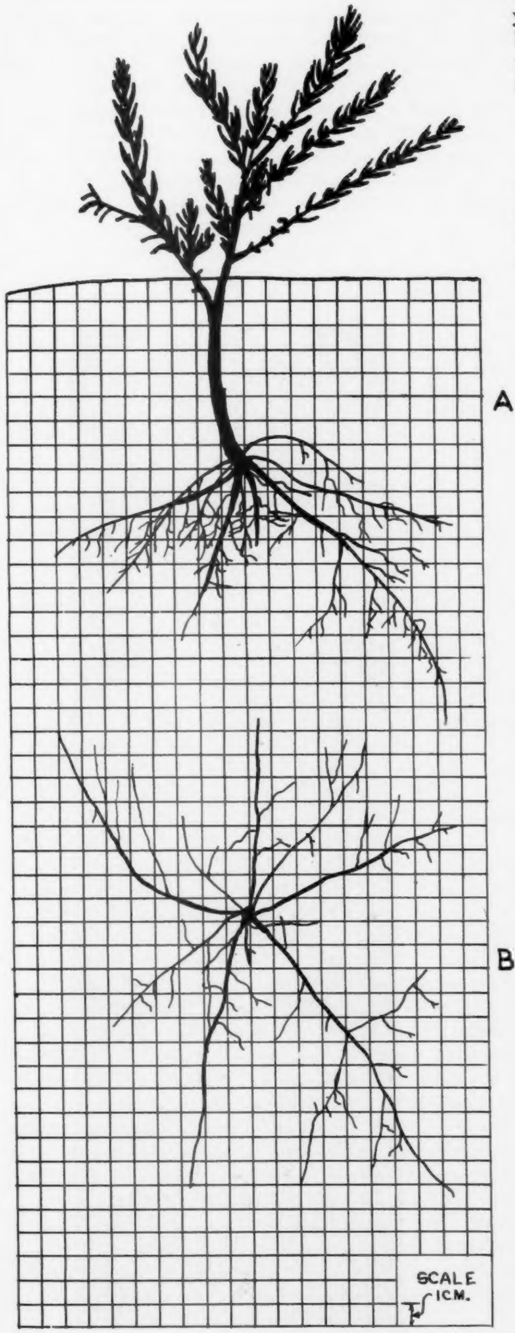
The stem is covered with thick-walled epidermis in which there are a few stomata. The cuticle is rather thick. A few collenchyma cells with chloroplasts occur beneath the epidermis but the rest of the cortical cells, about six rows in thickness, are parenchyma. Some fiber cells appear outside the primary phloem. The rest of the central cylinder consists of a cylinder of phloem, cambium and xylem to the inside of which are irregularly placed vascular bundles with large-celled pith parenchyma in the center. The older stem becomes very stiff and woody with its successive layers of xylem (Fig. 13D).

The root is covered by a layer of phellem with a band eight to ten rows of cortical cells inside. To the inside of this the anomalous structure is exhibited in incomplete strips of secondary phloem and xylem with fiber cells which fill the central cylinder, except for the primary vascular tissue in the center (Fig. 13E).

The plant is succulent or water-storing with abundant water-storage cells both in the leaves and the young stems. There is little air-storage space, except between the parenchyma and water-storage cells. This plant, therefore, is found growing on the upper littoral, as it cannot stand daily covering by salt water.

Limonium mexicanum Blake

Limonium is found on mud flats of the upper littoral associated with Salicornia, Distichlis, Monanthochloe, and Frankenia. It is not found in or near fresh water. It grows in both sand and clay, but is most abundant on clay mud flats. It can stand



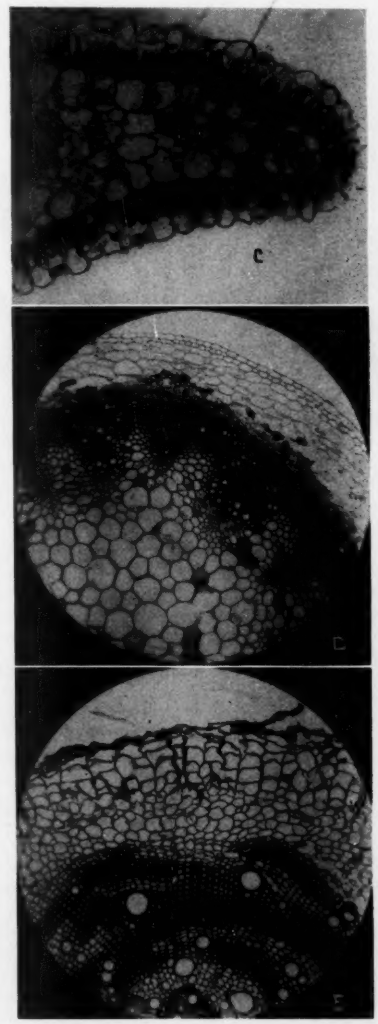


FIG. 13. *Suaeda californica* Wats.

A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of leaf.
D. Cross section of stem.
E. Cross section of root.

submergence during high or storm tides. Frequently debris lies around the plants. It grows scattered and is not found in pure stands. Counts per square meter show: Limonium 10, Salicornia (young plants) 3,500; Limonium 4, Salicornia 2,700; Limonium 12, Salicornia 3,400; Limonium 2, Suaeda 3, Salicornia 3,700, Frankenia 7.

The perennial plant starts as a single rosette and as it grows from year to year, the shortened stem branches and makes a cluster of rosettes which become higher and higher above the surface of the ground. Rosettes of ten plants averaged 9.6 cm. above the surface. Its height above ground including the flower stalks averaged 67.5 cm. with a spread of the rosette an average of 36.8 cm. (Fig. 14A).

The thick, entire, glabrous basal leaves have oblong-obovate blades. A leaf (blade and petiole) averages 21.3 cm. in length, while blades are 4.8 cm. wide at the widest part. The surfaces, particularly

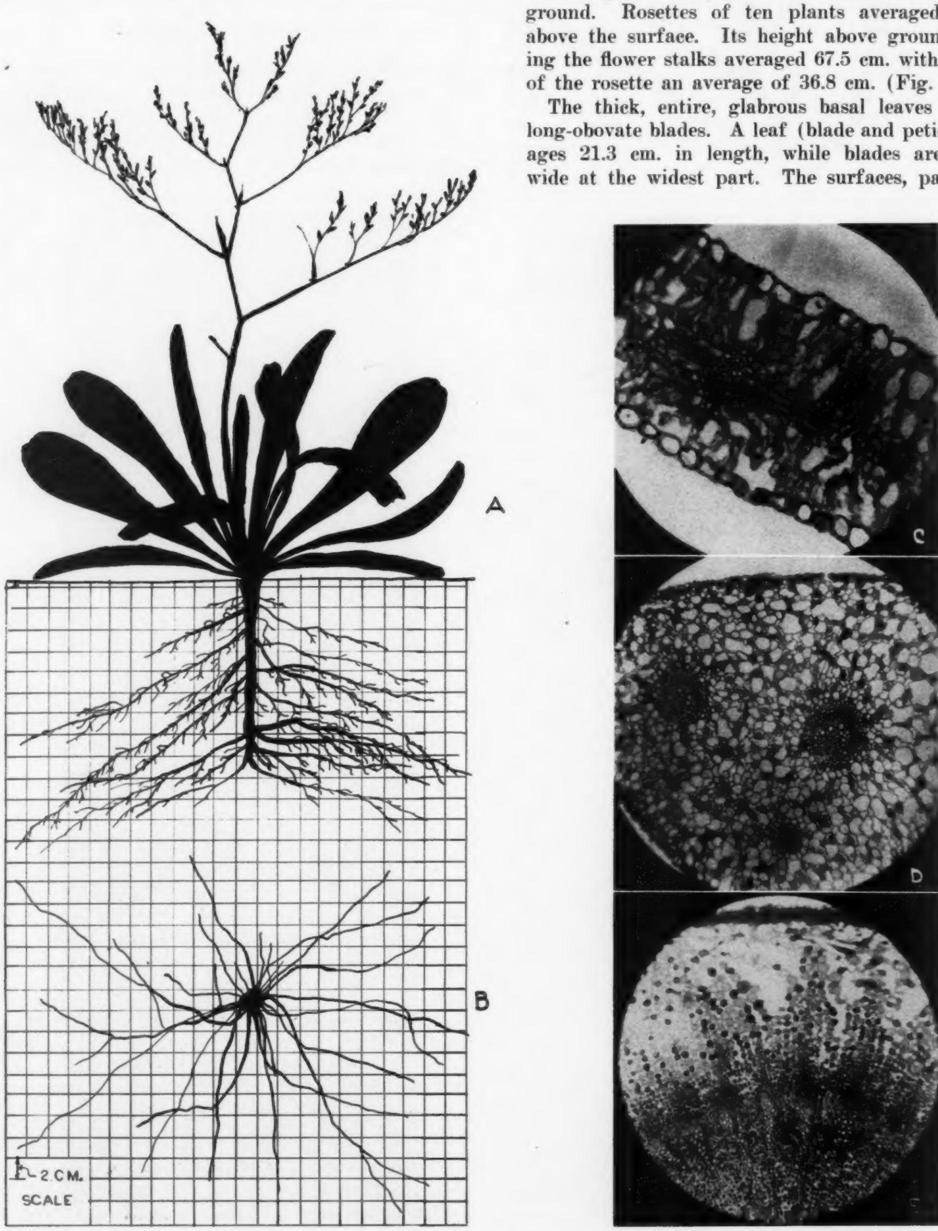


FIG. 14. *Limonium mexicanum* Blake.
A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of blade.
D. Cross section of petiole.
E. Cross section of root.

the lower, are heavily covered with a white chalky substance. It is practically stemless. The leaves afford some protection to those below them. The flowers are perfect, lavender, clustered at the ends of a much branched scape, both insect and wind pollinated. The fruit is an achene. The taproot is thick and reddish. It has a depth of about 30.0 cm. below the surface and a spread of up to 50.0 cm. In many plants excavated the fleshy taproot grew straight down for about ten centimeters, then divided sharply into four to six laterals. In higher locations, some taproots went down as deep as 25.0 cm. before branching. (Fig. 14B).

The upper epidermis of the leaf blade is covered with a thick layer of cuticle. The epidermal cells are varied in size, some eight times the contents of others. Both stomata and glands are found even with the surface. The chalk gland consists of a small group of epidermal cells made up of the gland cells and subsidiary cells. Solereder (1908) states that in most cases they excrete water and superfluous carbonate of lime salts on their external surface. No trichomes are present.

The mesophyll consists of one compact layer of palisade parenchyma tissue below the upper epidermis, one partly compact layer to the center of the leaf, veins and spongy parenchyma in the center, and irregular, loosely placed parenchyma (somewhat palisade in character) in the lower portion of the leaf. All of the parenchyma cells have chloroplasts. Air spaces are abundant in all the mesophyll except in the upper layer of palisade. Leaves are saturated with phlobaphene compounds. Young leaves have anthocyanin.

The lower epidermis of irregular-sized cells has abundant glands and stomata. The epidermis is covered with a thick layer of cuticle. No trichomes are present (Fig. 14C).

The petiole is fleshy and has numerous intercellular spaces between the chlorenchymatous cells which largely compose it. Vascular bundles, which vary in size, are abundant. Anthocyanin is present in many petioles (Fig. 14D).

The root is covered with a layer of phellem, inside of which are loosely placed cortical cells. Occasional tannin glands appear. The central cylinder consists of the usual arrangement of vascular bundles (phloem, cambium, xylem, and medullary rays) with pith parenchyma and many intercellular spaces in the center (Fig. 14E).

This plant, of the upper littoral, is adapted to infrequent submergence due to the storage of air in its leaves (both blade and petiole), and in its roots. In addition, it has the chalk glands whose chalky excretions act as a protection against excessive transpiration and consequently regulate the loss of water through the glands. Phlobaphene and tannin are also present.

Frankenia grandifolia C. & S.

Frankenia is a bushy, somewhat suffrutescent perennial, spreading from a center to cover an area as large as a square meter, as the older portions of the stem become decumbent and frequently root at the nodes. The average height above the ground is 33.8 cm. Frankenia appears to be one of the most adaptable of all the principal species, growing from places in salt water where it is submerged during high tides to positions as far as 160 cm. above the storm-tide limit as well as in several fresh-water areas. It is most luxuriant at about the high-tide limit. It is abundant in mounds of tidal trash. In its lower limits it has to compete with Salicornia; in its upper stretches with Distichlis, Monanthochloe, and others. Some counts per square meter were: Frankenia 28, Monanthochloe 8, Salicornia 4; Frankenia 90, Monanthochloe 175, Salicornia 3; Frankenia 85, Monanthochloe 18, Salicornia 7; Frankenia 660, Distichlis 70; Frankenia 744, Distichlis 70. It is sometimes found growing in pure stands, an average of 561 young plants to a square meter. Its best growth is in May; its poorest in December. Frankenia has Cuscuta growing on it. The plant stands full sunlight, although it is frequently shaded by its own kind or by plants competing with it.

The fascicled leaves of Frankenia are somewhat fleshy, the lower obovate and revolute, 1.2 cm. long and united into pairs by a membranous base. The upper leaves are oblanceolate, more revolute, 0.7 cm. long. The internodes average 1.4 cm. Counts of leaves of plants growing in aerated and in partly submerged locations showed that leaves of aerated locations averaged larger, 1.3 cm. for length (blade and petiole), width 0.68 cm., while in frequently submerged plants the counts were 1.2 cm. for length and 0.45 cm. for width. The perfect flowers are pinkish-purple and sessile. The fruit is a capsule. The root system, made up of numerous roots, is especially large when an aerial stem becomes buried and roots at the nodes (Fig. 15A and B).

The epidermis of the leaf is composed of very large cells (about one-sixth the diameter of the leaf). They vary in size and contain special glands which give off highly soluble salts. These salts, which are in part hygroscopic, cover the vegetative parts of the plants and aid in absorption of water (Solereder). Stomata are slightly sunken in the upper epidermis, which is covered with a thick cuticle. Small, plain, unicellular, unbranched, pointed trichomes are scattered over the surface, occasionally clustered.

The palisade cells are small, in two rows, and not very compact. The spongy parenchyma makes up about two thirds of the mesophyll. It has irregular-shaped chlorenchyma cells with numerous intercellular spaces and vascular bundles. Druses of calcium oxalate are present.

The upper and lower epidermal surfaces are very distinct, the former consisting of large cells fitted together as ordinary epidermal cells are, while the lower epidermis has cells half the size which join at the base of the cell and extend out as individual units. The stomata of the lower epidermis are numerous, recessed, and without subsidiary cells. The same type

of trichomes is present as on the upper epidermis (Fig. 15C).

The stem is covered with a thick layer of cuticle (about one-third the diameter of the epidermal cells). The epidermis is small, with occasional stomata. Plain, unicellular, unbranched, pointed trichomes are scattered over the surface. Older stems have a small development of cork about eight to ten rows in thickness. The rest of the cortex is composed of small-celled spherical parenchyma cells with many intercellular spaces. Almost a continuous band of fiber cells lies inside. The stele consists of phloem, cambium, and xylem separated by medullary rays. The

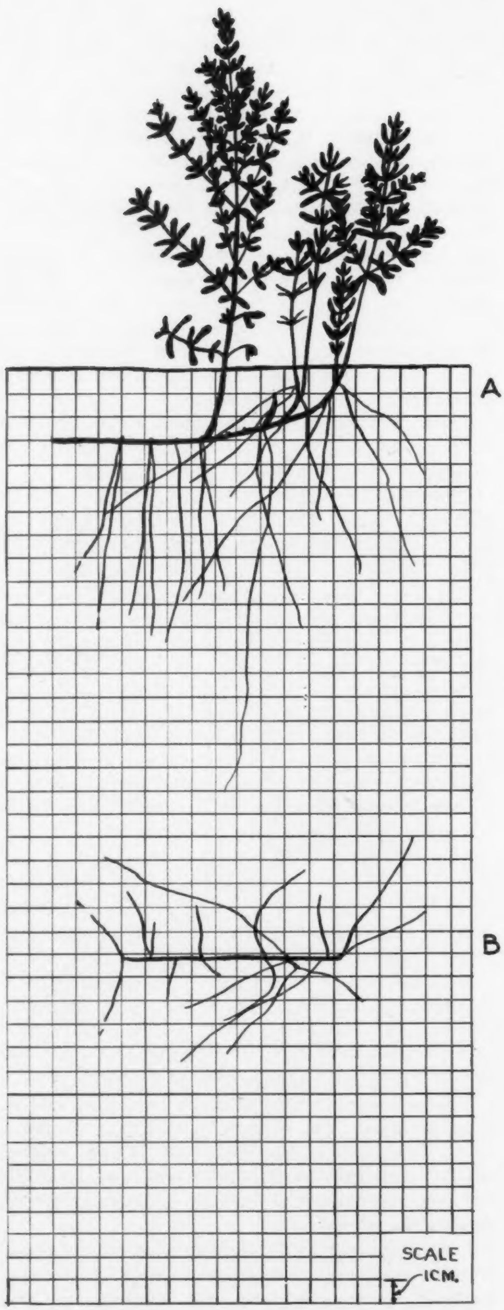


FIG. 15. *Frankenia grandifolia C. & S.*

A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of leaf.
D. Cross section of stem.
E. Cross section of root.

pith parenchyma has numerous intercellular spaces. Druses of calcium oxalate are present (Fig. 15D).

The root is tough with a thick layer of phellem. The cortical cells are small with intercellular spaces. Groups of sclerenchyma are placed regularly to the inside. The stele consists of phloem, cambium, and xylem separated by medullary rays (Fig. 15E).

In summary, Frankenia is adaptable to areas where it is frequently submerged, as well as in positions where the salt content of the soil is negligible. It has revolute leaves which reduce its transpiration. Secretion of salts by the glands probably reduces the salt content within the leaves and may aid in absorbing water. This function of the glands may be of significance in its existence in physiologically dry habitats. Air spaces in the leaves and stems make it possible for the plant to stand submerging and allow it sufficient aeration.

Atriplex watsonii Nels.

There are three species of Atriplex, the most abundant being *Atriplex watsonii* which is found in the upper littoral zone. It is a prostrate suffrutescent perennial forming large, tangled mats 1 to 3 meters across. It reaches a height of about 10 cm., and, instead of becoming taller, the branches become decumbent. It is found above the high tides but is frequently covered by storm tides. It grows in sand or in clay but does best in sandy soil or on tidal trash. It may be in pure stands, one to five plants to a square meter or associated with Frankenia, Distichlis, and Monanthochloe. Counts per square meter are as follows: Atriplex 2, Distichlis (aerial stems) 15, Frankenia 14; Atriplex 3, Limonium 6, Salicornia 2, Frankenia 26, and Suaeda 1; Atriplex 1, Frankenia 28.

Its leaves are white-scurfy, numerous, mostly opposite, and somewhat vertically placed. They are broadly ovate, averaging 1.4 cm. in length and 1.0 cm. wide. The stems are reddish, succulent and scurfy-covered, with internodes 2.8 cm. long. The flowers are dioecious, the staminate in naked terminal spikes, the pistillate, clustered and axillary. It is wind pollinated and wind disseminated. The root consists of a main or taproot with numerous secondaries (Fig. 16A and B).

The upper epidermis of the leaf bears large, overlapping stalked vesicles, giving a scurfy appearance to the leaf. The epidermis, covered by a thick layer of cuticle, is composed of rounded cells, about equal in size. The slightly sunken stomata are frequent. Below the epidermis are large water-storage cells. To the inside is one row of palisade composed of small cells, densely placed. The center of the mesophyll contains isolated vascular bundles around which are arranged larged food-storage cells. A row of somewhat irregular palisade and below a row of water-storage cells completes the mesophyll. Numerous druses of calcium oxalate are present. The lower epidermis is much like that of the upper in size, containing the same stalked vesicles and numerous stomata (Fig. 16C).

The young stem is covered with large overlapping vesicles, older stems with cork. The cells of the epidermis are small and the stomata are infrequent. To the inside of the epidermis, there are several rows of collenchyma, usually containing anthocyanin; and in young stems, chlorophyll is also present. The rest of the cortex is composed of typical parenchyma with many druses. Fiber cells occur in small groups just outside the primary phloem. The stele consists of secondary phloem and xylem with regularly placed variously sized vascular bundles, while the pith in the center is composed of large cells with numerous druses (Fig. 16D).

The root is covered with several rows of phellem cells. The anomalous structure common to this family is exhibited in the appearance of pericyclic rings or strips of cambium which soon lose their activity and form vascular bundles and conjunctive tissue. This structure fills the central cylinder except for some pith in the center (Fig. 16E).

Atriplex has few air spaces as compared to the other principal species and can, therefore, stand but little submerging. It can succeed in the upper littoral because of its salt content, as it is abundantly supplied with druses of calcium oxalate. Its evaporation may be checked by its vesicles which form a dead-air space next to the epidermis.

SUMMARY

Of the nine species chosen for anatomical examination, there is a range from one which grows in standing water to those which bear covering only at infrequent intervals. In Spartina, which stands the greatest salt-water immersion, it is found that it has the largest air spaces in the leaves, stems, and especially in the rhizomes and the roots. With this supply, continued aeration from outside air, at least to its underground parts, is not so essential. It grows particularly well in the shallow water of large bodies of water, the salinity of which is only slightly variable throughout the year. Its xerophytism is shown in its rolled leaves. In these three respects it is in contrast to Salicornia, which does not bear as much submergence. The plant has some intercellular spaces, but they are less abundant than in Spartina. It grows in situations where the salinity not only is more variable but may be much greater. Its xerophytism is shown in its absence of leaves, and its succulence. On the whole, it is the most versatile of all the principal genera. Taylor (1939) shows in his experiments that outstanding salt-marsh plants grow in such places not from preference but from necessity. Spartina grew best in low salinity, while Salicornia, with a salt tolerance from 1.015 to 1.022, grew best in the culture at 1.022.

Monanthochloe and Distichlis, although grasses, and growing in the same littoral areas, are easily distinguishable externally. Their anatomy is, however, very similar; and they may be considered together. Spreading by means of their aerial stems and rhizomes, they are aggressors in areas where aeration in the soil is improved, but where salinity

is a marked feature. They do not have the abundant air spaces of Spartina, nor the succulence of Salicornia. They are successful in their physiologically dry habitat because of their rolled leaves, and they can stand some submergence because of the frequent intercellular spaces of their subsurface parts.

Batis and Suaeda have succulent leaves. Both are able to stand submerging for a limited time. They have comparatively few air spaces. They are able to maintain themselves because of their succulence.

Limonium stands as an example of a rosette plant, not very aggressive, being able to grow successfully on mud flats where there is not much aeration. It is unlike any of the rest also in that it is broad-leaved and practically stemless. It has many air spaces in the mesophyll of the blade and in the petiole, as well as in the root. It can stand occasional submergence and grows where the salt content is considerable but the aeration only fair. It may be that it is so successful because the chalky excretions of its glands are a protection against water loss through excessive transpiration.

Frankenia has revolute leaves. Many small air spaces are found both in the mesophyll of the leaf and in stem and root. In addition, it has glands which secrete salts and may help to reduce the salt

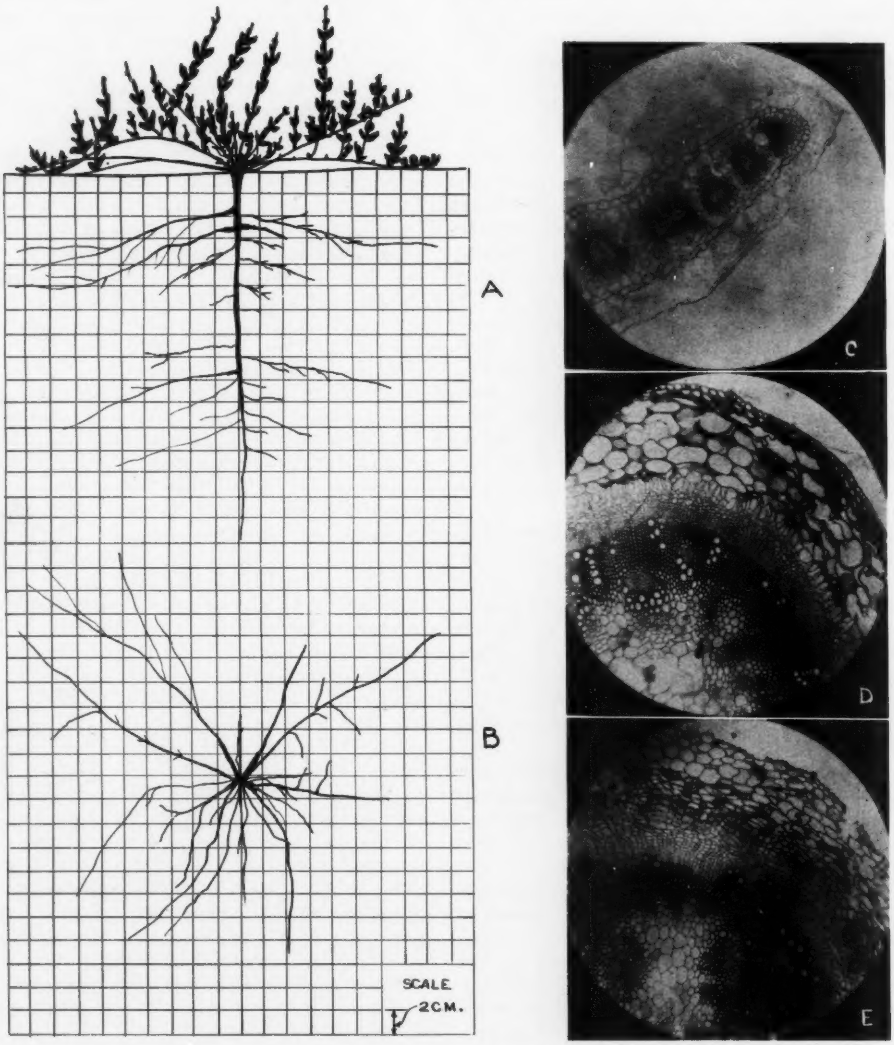


FIG. 16. *Atriplex watsonii* Nels.

A. Vertical section of plant.
B. Horizontal view of root system.
C. Cross section of leaf.
D. Cross section of stem.
E. Cross section of root.

content of the plant. It has calcium oxalate druses. It is an adaptable plant growing where it gets frequent submerging, but doing best when submerged only by storm tides.

Atriplex is a succulent because of its leaves which contain abundant water-storage cells. The surfaces of the leaves and the stems are heavily covered with large vesicles. Druses of calcium oxalate are present. The plant has sufficient air-storage spaces for only occasional submergence and can maintain itself successfully because of its succulence.

CONCLUSIONS

1. Twelve stations in definitely saline areas of San Diego County represent the various conditions under which the salt marsh vegetation exists.

2. The marshes may be placed in three groups. (1) with large bodies of water, open to the ocean, where salinity is almost constant, (2) with fresh-water streams flowing through most of the year, in which salinity fluctuates, with low percentages during the rainy season, and (3) small areas closed to the ocean most of the year, stream flow only during rainy season, where the salinity range is great, reaching high percentages during summer and autumn.

3. Large bodies of water are less saline than small bodies, with the soil near large bodies less saline than the soil around small bodies. The inrush of tides and evaporation tend to make the areas saline. Precipitation, flow of fresh-water streams, seepage from irrigation and gradual rise in land level tend to make the soil less saline. The free water at 10 cm. depth in marsh communities is usually more saline than the water at the same depth in adjacent bodies of water. Soil and water temperatures fluctuate little, with a range from 14° to 27°C. Light is intense, all plants stand direct light.

4. Bare areas show such high concentration of salts in the surface layers that species are prevented from entering such an area except during periods of winter rains and immediately following.

5. Ditching aids in the improvement of aeration and freedom from competition. This results in large-sized salt-marsh plants along its edges.

6. Lacking frost, the growing period is throughout the year, its peak immediately after the winter rains. Flowering occurs largely in the summer months.

7. There are three general areas of plants. (1) lower littoral, in which the principal species is Spartina, (2) the middle littoral, in which the principal species is Salicornia, and (3) the upper littoral, in which there is competition among a number including Frankenia, Distichlis, Atriplex, and Monanthochloe.

8. Spartina, a xerophytic grass, with rolled leaves, propagating principally by rhizomes, stands the greatest salt-water immersion, as it has abundant intercellular spaces and lacunas. Salicornia, a leafless halophyte, does not bear as much submergence as Spartina although it grows in situations where the salinity is more variable. It has a limited amount of air stored in its intercellular spaces and air-storing tracheids. Monanthochloe and Distichlis, of the upper littoral, both grasses with rolled leaves and propagated by runners and rhizomes, have air spaces in their subsurface parts sufficient to stand some submergence. Batis and Suaeda both with succulent leaves stand submerging for a limited time as they have comparatively few air spaces. Limonium, a rosette plant, grows successfully on mud flats with poor aeration as it has intercellular spaces in blade, petiole and root. Frankenia, of the upper littoral, has revolute leaves, many small intercellular spaces and abundant glands which excrete salts over the leaf surface. It is adaptable to submerging but does best just below the storm-tide level. Atriplex, a succulent, is heavily covered with vesicles and has few air spaces as compared to the previous eight species and, therefore, can stand but little submerging. Algae and other aquatic species, such as Ruppia, play a very small part in the marshes.

9. Of all the biota, man has wrought the greatest changes through drainage and fill.

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